# Spatio-temporal change in species and morphological diversity of reef fishes in the South Pacific Ocean

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# General Abstract

The geography of the South Pacific, with its numerous oceanic islands, offers a unique opportunity to examine prevailing theories on the accumulation and maintenance of biodiversity. It is well recognised that for most taxonomic groups, species richness declines poleward from the equator and eastward across the South Pacific. However, as ocean temperatures warm and oceanographic barriers move with climate change, shifts in the ranges of tropical species towards higher latitudes may lead to changes in community structure and resilience in subtropical locations. Here, I examine the existing biodiversity gradients of reef fishes across the South Pacific Ocean, and identify potentially climate-induced temporal shifts of tropical species into the high latitude and isolated Rangitāhua archipelago. Furthermore, I examine morphological changes across latitude and longitude to identify traits associated with species colonisation ability and function within the often species depauperate communities in more isolated and southerly regions of the South Pacific. Additionally, I examine how morphological changes over time might impact the morphological space of the fish community at Rangitāhua. I assessed morphological change in 12 standard measurements for 948 fish species, from nine families found on the reefs surrounding 19 of the major island groups of the South Pacific Ocean. I found that while species richness followed the predicted decline towards the east and south, morphological diversity showed the opposite trend, increasing east and south. Furthermore, similar morphological changes were evident with body size and pre-orbit length increasing in response to both latitude and longitude, although more significantly with longitude. Despite this, analysis of individual families revealed unique patterns of morphological change within the South Pacific Ocean, may be indicative of the differing strategies of each family to colonise and persist in more southerly and easterly locations. Within Rangitāhua, using a list of 149 shallow Teleost fishes including the dates of their first sighting, I identified a temporal shift in the biogeographic affinities of the fish assemblage with an increasing contribution from tropical regions over time. Newly discovered, more tropical species, only occurred in low numbers, possibly because they are still in the early colonising stage or because the islands environment is still more temperate than these fish require to increase in abundance significantly. Despite also finding that the morphological diversity of the fish assemblage changed through time, morphological change was not directional, indicating that although new species are arriving, their morphology is similar to longer-established, more temperate fishes. Therefore, although the frequency of species with tropical biogeographic affinities is increasing over time at Rangitāhua, this is not strongly impacting the community's morphological variation. My results for Rangitāhua support the global pattern of tropical species re-distributing towards higher latitude region over

time. Overall, my thesis examining both species and morphological change in reef fishes across large-scale geographic gradients within the South Pacific Ocean provides insight into potential future biodiversity changes and may allow us to predict which species are likely, or capable of extending their ranges towards the poles.

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# Chapter 1: General Introduction

## 1.1 Rationale for study

Geographic patterns of species richness are among the most studied ecological phenomena. Since the 19th century, scientists have examined species diversity change among locations leading to several well-known gradients in the distribution of biodiversity on our planet. Possibly the best recognised biodiversity gradient is the relationship between species diversity and latitude (Fischer, 1960; MacArthur, 1965; Pianka, 1966; Wallace, 1878). That is, equatorial locations hold the highest species diversity, and species diversity declines with increasing latitude. Similarly, the theory of island biogeography (MacArthur & Wilson, 1967) identifies patterns of species richness on islands in accordance with distance or isolation of an island as well as island age, size and shape. Often, there are competing explanations for biodiversity gradients, and so identifying the mechanisms underlying the patterns observed in nature is important.

While latitude itself has little effect on organisms, environmental factors correlated with latitude, are known to cause a biodiversity change. For instance, increased solar energy in low latitude regions leads to a rise in primary productivity, ensuring resources are more stable and predictable which enables more energy to support more individuals and species within the community (K. L. Evans, Warren, & Gaston, 2005; Fraser & Currie, 1996 ; Hawkins *et al.*, 2003; Turner, Gatehouse, & Corey, 1987; Wright, 1983). Furthermore, with a more stable environment, populations can specialise, resulting in narrower niches and may eventually lead into speciation events (Cowman *et al.*, 2017; Kozak & Wiens, 2007, 2010; Mora *et al.*, 2003). Conversely, high latitude regions with less solar energy are much colder, and fewer species are able to tolerate these more extreme conditions (Sunday, Bates, & Dulvy, 2011). Due to these environmental factors correlated with latitude, low latitude regions have not only been considered the origin for many lineages, but also the centre of survival during glacial periods (Bowen *et al.*, 2016).

The theory of island biogeography has played a critical role in advancing our understanding of the rate and type of biodiversity accumulated on islands. The theory explains that if any unoccupied space is made available (e.g. volcanic islands and slips) this new space is colonised via dispersal. The proximity of this newly colonisable space to areas of higher diversity will dictate the rate of species richness accumulation as explained by the species-distance relationship (Warren *et al.*, 2015). For example, richness decline of land birds in Wallacea and the West Indies archipelagos are related with islands increasing distance (Dalsgaard *et al.*, 2014) and in reef fishes with increasingly isolated islands within the Indian Ocean having fewer species (Hobbs *et al.*, 2012). With increasing distance, colonisation success diminishes, but given enough time, species will still find their way. That is, the older an island the more species it is likely to accumulate (Hachich *et al.*, 2015; White *et al.*, 2006). Furthermore, larger patches provide a larger target and they tend to have a higher biodiversity when compared to smaller patches because of the species-area relationship (Lomolino, 2000). Last, the geographical complexity of a patch, influences habitat diversity, allowing more niches to be occupied and increasing species richness (Hortal *et al.*, 2009; Stein, Gerstner, & Kreft, 2014). For example, within the Canary archipelago, islands with more elevation have a greater habitat diversity and showed an increase in species richness relative to other islands (Steinbauer & Beierkuhnlein, 2010). Identifying patterns of island biogeography assist in understanding factors that influence species richness over large scales.

There are also well-known geographic trends in the morphology of species with respect to latitude and attributes of islands. From Bergmann's (1847) to Allen's rule  (1877), larger and rounder endothermic animals retain heat better than smaller animals and hence there is a tendency for larger size at higher latitudes (Meiri & Dayan, 2003). Additionally, the island effect (Foster, 1964) is known to cause an increase or decrease in body size depending on available resources for an optimal body size (Lomolino, 2005). However, there are some morphological trends that are influenced directly by gradients in species richness. In particular, within areas of high biodiversity, increased morphological variation can support niche diversification and resource specialisation (Mason *et al.*, 2008). For example, the cichlid populated Tanganyika Lake has led to several adaptive specialisations in relation to diet to reduce competition within the populated lake (Takahashi & Koblmuller, 2011). Therefore, within highly biodiverse regions we might expect to see higher morphological variation, whereas areas with low species richness may drive species to morphologically converge due to filling similar niches.

The marine environment is the largest biome on Earth. Unsurprisingly then, the biodiversity gradients we see on land are also apparent in the sea (Bellwood & Hughes, 2001; Bellwood, Meyer, & McDowall, 2009; Connolly, Bellwood, & Hughes, 2003; Tittensor *et al.*, 2010). Presumably, marine organisms are bound to similar environmental restrictions as terrestrial organisms. Indeed, similar morphological changes occur latitudinally within both terrestrial and marine environments. For example, increasing body size towards the poles for species in both environments (Blanck & Lamouroux, 2007; Kingsolver & Huey, 2008). However, factors influencing these morphological changes may differ. For instance, body size increases poleward for endothermic organisms relate to reducing heat loss (Bergmann, 1847), while for ectothermic organisms this increase relates to a slower growth and maturation rate in colder temperatures (Atkinson, 1994; Ray, 1960). Furthermore, body size is correlated with environmental tolerance (Luiz *et al.*, 2012), hence an increase in this trait may be a consequence of selective pressures towards high latitudes.

Eastward across the Pacific, and west into the Indian Ocean there is a decrease in marine species richness, likely as a consequence of reduced colonising success with increasing distance from highly diverse areas. Specifically, for taxa unable to survive in open water, habitable areas exist as hotspots for biodiversity within the marine environment (Bellwood & Hughes, 2001). In particular, coral reefs offer a centre of survival for a large number of organisms (Bellwood *et al.*, 2015; Bellwood *et al.*, 2009; Tornabene *et al.*, 2015). Furthermore, with several lineages originating from extremely diverse reef areas (Cowman & Bellwood, 2013; Mora *et al.*, 2003), organisms are known to have a close history with coral species (Bellwood & Wainwright, 2002)**.** Therefore, it is not surprising that coral reefs represent complex ecosystems with the highest biodiversity in the world, especially for the immensely diverse Teleost taxa (Bellwood & Wainwright, 2002). Furthermore, from past extinction events coral reefs have served as a refuge for many species (Cowman & Bellwood, 2013; Cowman *et al.*, 2017). For example, previous global heating and cooling events have led to the rise and drop of sea levels, however, areas such as the Indo-Pacific Archipelago have remained relatively stable for coral habitat ensuring the survival of the coral ecosystem with all living organisms within it (Bowen *et al.*, 2016). This long history of species surviving and originating within this area has created an extremely rich abundance of corals and fishes in the central indo-Pacific, from which species have colonised the Eastern and Southern Pacific.

The Pacific Ocean has more islands than every other ocean combined (Gillespie, Claridge, & Roderick, 2008), and as islands become more distant from the dominating western landmasses and from each other, species richness declines for a number of taxa (Bellwood & Hughes, 2001; Connolly *et al.*, 2003; Mora *et al.*, 2003). Associated with this species richness decline, we may also see a change in morphological diversity and potentially a change in species morphological traits, particularly those that assist a species in colonising remote islands. For instance, in plant species larger seed size gives an increased dispersal potential, while taller plants give an increased persistence potential (Auffret *et al.*, 2016). With certain traits known to benefit the dispersal and persistence of marine organisms across latitude and longitude, evidence for a higher proportion of these morphological traits are evident within the marine communities. For instance, body size of marine fishes is known to increase fecundity, thus improving odds for colonisation success for isolated regions longitudinally (Barneche, Robertson*, et al.*, 2018; Bender *et al.*, 2013). Furthermore, larger body size increases the potential variety of prey items and reduces the likelihood of predators in different community compositions along the latitudinal axis (Bellwood & Wainwright, 2002; Jacquet *et al.*, 2017). As a result, isolated islands are known to have a higher proportion of larger bodied fish when compared to highly diverse interconnected islands (Jacquet *et al.*, 2017). Across the South Pacific and into the East Pacific, spatial patterns in species morphology may help identify processes shaping patterns of species richness. Furthermore, morphological changes in fishes over time may help us understand what changes we might see under climate changes.

Ongoing climate changes is causing global redistribution of organisms with large impacts to higher latitude regions as community compositions shift from temperate to tropical. In particular, for marine coastal ecosystems, range shifts poleward are occurring faster than terrestrial environments (Burrows *et al.*, 2011; Poloczanska *et al.*, 2013) and high latitude areas are vulnerable to the effects of climate change (Assis, Araujo, & Serrao, 2018; Nakamura *et al.*, 2013). It is thought that a combination of regional and local ocean warming, and changes in ocean circulation and strength of associated currents may be driving this redistribution of biodiversity. Indications of community changes are evident in the North Sea (Beare *et al.*, 2004) and Tasmania as tropical species advance towards the poles (Last *et al.*, 2011). Alongside these new arrivals, new functional groups can cause detrimental effects to temperate communities and can lead to a complete change in the functionality of the ecosystem (Davis & Shaw, 2001; Verges *et al.*, 2014). Detecting range shifts will help identify ecosystems changing and assist in recognising future patterns of climate change.

## 1.2 Overview of Thesis

This thesis is composed of four chapters. Chapters two and three are written in manuscript format and I anticipate submitting these for publication soon after receiving my thesis examiner's comments. Consequently, there will be some repetition of the content and methodological detail among the four chapters presented in this thesis.

In Chapter two I examine gradients in species and morphological diversity for nine reef fish families across the South Pacific Ocean. Morphological traits that improve colonising success for reef fishes are known to be correlated with species richness (Bender *et al.*, 2013; Jacquet *et al.*, 2017). However, despite well recognised patterns of species richness for reef fish along latitude and longitude within the Pacific Ocean (Bowen *et al.*, 2016; Connolly *et al.*, 2003), changes in morphological diversity along these gradients is poorly understood. First, I test the relationship between overall species richness and morphological diversity, and then examine this relationship for each family. I then investigate morphological change across latitude and longitude for each family, and test for coordinated morphological changes among families. I expect a decrease in morphological diversity towards the poles and eastwards within the South Pacific Ocean and morphological changes will differ between families. Recognising patterns of species richness and relating them to morphological diversity and morphological changes across latitude and longitude will provide an understanding of the determinants if reef fishes assemblages within the South Pacific.

In Chapter three I examine the temporal changes in community composition of fishes at the subtropical archipelago of Rangitāhua, or the Kermadec Islands, as one of the most isolated regions in the South Pacific Ocean. With each expedition, new species are recorded within the area. These additions to the fish biodiversity of Rangitāhua may be the result of increased sampling, or alternatively, may be the consequence of climate induced species redistributions. Here, I examine the changing biogeographic affinities of fishes at Rangitāhua and investigate if Rangitāhua is undergoing tropicalisation using a reef fish species list stratified through time by species' first observation. Furthermore, I explore temporal changes in morphological variation as a result of the fish assemblage changing through time, and assess whether certain fish species groups (i.e. tropical or not) are more abundant than others on these high latitude reefs. Identifying changes in the biogeographical affinities and morphology of fish assemblages in Rangitāhua may inform potential impacts of climate change on high latitude, isolated islands, allow us to predict how other geographic areas may be affected.

In Chapter four I synthesise the results of Chapters two and three. I provide insight into species richness and morphological gradients within the South Pacific and temporal changes of community within Rangitāhua. I discuss the limitations of my study with reference data collection and the boundaries of plausible assumptions that can be made from my study. Last, I suggest future directions for continuous monitoring and data collection of islands to identify changes in species richness and morphological diversity to predict patterns of climate change.

# Chapter 2: Morphological change across gradients of latitude and longitude for reef fishes of the South Pacific Ocean

## 2.1 Abstract

The Pacific is the world's largest ocean. Within the Pacific, the geography of the South Pacific, with its numerous oceanic islands, offers a unique opportunity to examine prevailing theories regarding the role of environment, geography, and in particular isolation on biodiversity patterns. It is well recognised that for most taxonomic groups, species richness declines poleward from the equator and eastward across the South Pacific. Here, I examine another dimension of the South Pacific biodiversity gradient, evaluating the morphological diversity of reef fishes. Fish morphology has previously been associated with species colonisation ability and their function within reef assemblages. Here, I contrast the potential impact of diminishing niche breadth with latitude versus the influence of increasing isolation and associated filtering of the species pool into the east Pacific. I assessed the morphological diversity and patterns of morphological change based on 12 standard measurements for 948 fish species (from nine families) found on the reefs surrounding 19 islands of the South Pacific Ocean. I found that morphological diversity had an inverse relationship to species richness, with morphological variation increasing towards the east and south. Moreover, although increasing latitude and longitude were associated with similar changes in morphology, longitude appeared to have a stronger effect on morphological change in reef fish assemblages of the South Pacific, whereby fishes associated with higher latitude and more eastern islands were longer, had deeper bodies, and in particular had longer pre-orbital lengths. However, examining the association of latitude and longitude, with morphological change at the family-level, I found that morphological changes were not concordant among families. Understanding how reef fish morphology changes along different environmental gradients, and whether morphological diversity predictably scales with species richness, may provide us with insight regarding consequences of species gains and losses due to local impacts and global change causing the re-distribution of species.

## 2.2 Introduction

The correlation between species richness and latitude, where species richness is greatest at the equator and declines toward the poles, is arguably the most recognized and well supported global biodiversity patterns (Fischer, 1960; Pianka, 1966). While latitude itself has little effect on organisms, several factors correlated with latitude are the suggested drivers for the poleward decline in species richness. For example, at low latitudes, there is more energy, and therefore more organisms can be supported from an increase in primary production (Fraser & Currie, 1996 ; Hawkins *et al.*, 2003; Turner *et al.*, 1987; Wright, 1983). Additionally, low latitude regions have been more stable through geological time, allowing more time for speciation and species accumulation without extinction resulting in increases in biodiversity in these regions (Bellwood & Wainwright, 2002; Cowman & Bellwood, 2013; Cowman *et al.*, 2017; Kozak & Wiens, 2007, 2010; Mora *et al.*, 2003). As a consequence of high species diversity, low latitude regions are also suggested to have greater competition (Shepherd, 1998), driving heightened resource partitioning and specialisation and further fuelling relative increases in biodiversity (Mason *et al.*, 2008).

The sheer increase of species and biomass at low latitude, as well as the increased resource availability, and competition for resources, may drive patterns of morphological diversity to follow the same trend as species richness. In some cases, declines in morphological diversity are the result of converging morphological strategies for living in certain environments (Stayton, 2006). For example, following Bergmann’s (1847) and Allen’s (1877) rules, homoeothermic animals become larger and their limbs get proportionately smaller at higher latitudes and altitudes to enhance heat retention. Similarly, vascular plants are often shorter and have thicker leaves to reduce frost damage in colder climates experienced at higher latitudes and altitudes (Hulshof *et al.*, 2013). Thus, gradients in morphological diversity can be concordant with species diversity gradients, and the ways in which species morphology changes along these gradients may be consistent among species groups.

The Pacific Ocean is one of the most extensive realms on our planet, and within the Pacific Ocean, shallow reef biodiversity follows the well-known poleward decline of species richness (Bellwood & Wainwright, 2002; Connolly *et al.*, 2003; Mora *et al.*, 2003; Sanciangco *et al.*, 2013; Tittensor *et al.*, 2010). The putative drivers of the latitudinal species richness gradient in the sea are similar to those underlying global biodiversity trends, for example, temperature and stability (Barneche, Rezende*, et al.*, 2018; Gaston, 2000). However, there is a second well-documented gradient in species richness in the Pacific, where the greatest richness in found in the western Pacific and declines towards the east (Bellwood *et al.*, 2009; Mora *et al.*, 2003). The Indo-Australian archipelago (IAA) in the western Pacific, is considered the centre of origin for most shallow marine species, and/or lineages in the Pacific (Bellwood *et al.*, 2015; Cowman & Bellwood, 2013; S. M. Evans *et al.*, 2016), and the eastward decline in species richness across the Pacific, is often attributed to increasing isolation from the IAA and declines in reef area (Bellwood & Hughes, 2001; Connolly *et al.*, 2003).

Few studies have examined patterns of morphological diversity within the Pacific Ocean. Across latitude, morphology of ectothermic marine species is likely influenced by the environment and competition in similar ways to that observed in terrestrial landscapes. Recent studies have also reported that morphology is an important determinant of a species ability to colonise remote locations (Barneche, Rezende*, et al.*, 2018; Barneche, Robertson*, et al.*, 2018; Jacquet *et al.*, 2017; Luiz *et al.*, 2013). For instance, in reef fishes there is a correlation between colonising success with body size (Jacquet *et al.*, 2017; Luiz *et al.*, 2013; Luiz *et al.*, 2012), It is thought that increasing body size can improve fecundity, reduce predation, and increase competitiveness (Andersson, Johansson, & Soderlund, 2006; Barneche, Robertson*, et al.*, 2018; Bender *et al.*, 2013). Furthermore, body size is correlated with gape size, thereby increasing the range of prey that could be consumed (Goatley & Bellwood, 2009; Ladds *et al.*, 2020; Nilsson & Brönmark, 2000). Therefore, there may be a longitudinal decline in morphological diversity across the Pacific Ocean as marine species converge on morphologies that are important for successful colonisation of remote locations. Such a concerted morphological change may be expected to contrast with the direction of morphological change seen across latitude.

In this study I document morphological diversity and analyse morphological changes across the South Pacific Ocean for nine fish families commonly associated with reef ecosystems. Reef fishes in the Pacific Ocean are highly speciose, and have a variety of morphological traits that are uniformly measurable across diverse families. However, given the diverse niches occupied by fishes in these families, I might expect morphological traits to be selected in different directions in different families. First, I test whether morphological diversity of reef fishes follows the overall trend in species richness, and then examine relationships between species richness and morphological diversity for each family independently. I then investigate morphological change across latitude and longitude for each family, and test for coordinated morphological changes among families. I expect that morphological diversity will decrease toward the south, and east within the South Pacific Ocean; however, I anticipate divergent changes in fish morphology across latitude and longitude. My analysis provides insight into the relative roles of temperature (across latitude) and isolation (across longitude) in shaping morphology for a diverse array of fish assemblages found within the Pacific Ocean.

# 2.3 Methods

## 2.3.1 Sample locations and shallow reef fish species lists

I focused on nine families of fishes commonly associated with shallow reef ecosystems and representative of the diverse functions and morphology of fishes commonly inhabiting reefs. Specifically, the nine families considered were: Acanthuridae, Apogonidae, Blenniidae, Chaetodontidae, Gobiidae, Labridae, Pomacanthidae, Pomacentridae, and Scariidae. My area of interest spanned the major island groups and land masses of the South Pacific (figure 1), from tropical Eastern Australia in the west to Rapa Nui/Easter Island, Chile in the east (145.78°W to -109.3°E) and from Papua New Guinea in the north to Lord Howe Island, Australia in the south (-5.22°S to -31.56°S). A list of countries within the study area, for which lists of resident fishes were available was retrieved from Fishbase (Froese & Pauly, 2019) using the rfishbase R package (Boettiger, Lang, & Wainwright, 2012). Specifically, I used the 'country' function and the 'family' argument to retrieve location-specific species lists for the nine fish families (removing species that were labelled as 'misidentified', 'questionable', and 'in the non-marine environment' for each location). I then excluded countries with non-contiguous, or non-discrete extents, such as French Polynesia (including Marquesas); instead, opting to use discrete locations (e.g. Tahiti) as sample locations. For cases where sample locations were nested within a country or region I wished to retain, I refined and separated the species lists based on published articles. For instance, to ensure that any species endemic to either Lord Howe Island or Norfolk Island were not included in the species list for Australia, I removed island endemics from the Australian species list using Francis (2019) as a reference. For countries that extended beyond my area of interest (such as Australia and Papua New Guinea), I queried the occurrence records for each species in the Ocean Biogeographic Information System (OBIS, 2019) using the 'occurrence' function of the R package Robis (Provoost, Bosch, & Appletans, 2017). If the species did not occur within my area of interest (e.g. species only occurring in southern or western Australia) it was removed from the species list for that sample location. In cases where no records for a species were retrieved, I would additionally search for the species occurrence records in OBIS using all synonyms listed in Fishbase. To ensure my species lists included only shallow reef fishes for each family, I queried the maximum recorded depths for each species retrieved using the 'occurrence' function of Robis, and removed species that only occurred at depths greater than 50m. Last, sample locations were retained only if they had at least 30 species recorded across the families of interest (figure 1). My final dataset included shallow reef fish species lists for 19 sample locations (figure 1).

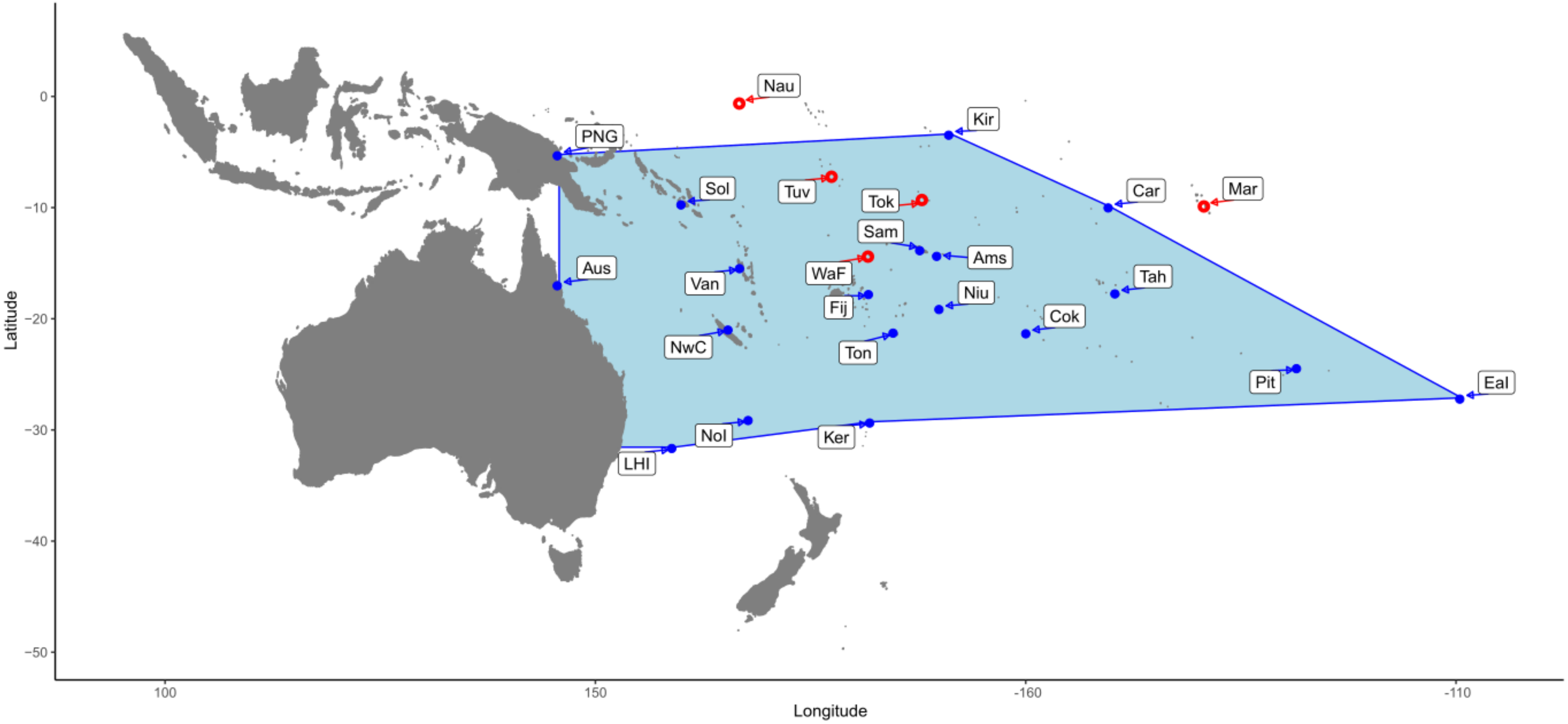

**Figure 1** Map of sample locations for which fish species lists were queried for nine fish families. The nineteen locations retained for analysis (blue dots) included: Papua New Guinea (PNG), North-eastern Australia (Aus), Solomon Islands (Sol), Vanuatu (Van), New Caledonia (NwC), Lord Howe Island (LHI), Norfolk Island (NoI), Kermadec Islands (Ker), Fiji (Fij), Tonga (Ton), Kiribati (Kir), Samoa (Sam), American Samoa (Ams), Niue (Niu), Cook Islands (Cok), Caroline Island (Car), Tahiti (Tah), Pitcairn Islands (Pit), and Easter Island (EaI). The five locations that did not meet the minimum criteria to be included in the analysis (red dots) included: Nauru (Nau), Tuvalu (Tuv), Wallis and Fortuna (WaF), Tokelau (Tok), and Marquesas (Mar).

### 2.3.2 Morphological measures of fish species

To analyse morphological changes of reef fishes across the South Pacific I used the 'morphometrics' function in Rfishbase to extract morphology data for the fish species found at my sample locations. The morphological measures provided by Fishbase include the commonly measured features of fishes used for taxonomy, ecomorphology, and several fish functional traits (Villéger *et al.*, 2017). After excluding species for which measures were based on hand-drawn images (rather than photographs of specimens), and species with large amounts of missing data, we were able to retrieve morphological measures for a total of 948 species. The amount of data missing for each location (i.e. the percentage of species that were excluded from the species list because there were no morphological measures) was similar across sample locations and ranged between 22.1% and 4.3% for all families (appendix 1). Where photographs, and thereby morphological data, were available for more than one specimen per species, I used the largest available specimen to increase the likelihood of capturing morphological variation among adult fishes.

I transformed the morphological measures into proportions so that I could focus on relative shape changes across species. Specifically, head measures: eye diameter (ED) and pre-orbit length (POL) were standardised by head length (HL); and body measures: standard length (SL), head diameter (HD), pre-anal length (PAL), pre-dorsal length (PDL), pre-pelvic fin length (PPL), pre-pectoral fin length (PPEL), body depth (BD), caudal height (CH), caudal length (CL), caudal fork length (CFL) were standardised by total length (TL). Although, some studies have used SL (rather than TL) to standardise body measures, there are unclear guidelines for measuring SL and studies have shown that measurements of TL have significantly lower average error than SL (Howe, 2002). Nevertheless, preliminary analyses indicated that the trends in my dataset were consistent among standardisation methods, including: standardising body measures to SL and head measures to HL; standardising body measures to TL and head measures to HL; standardising tail measures to TL, body measures to SL, and head measures to HL.

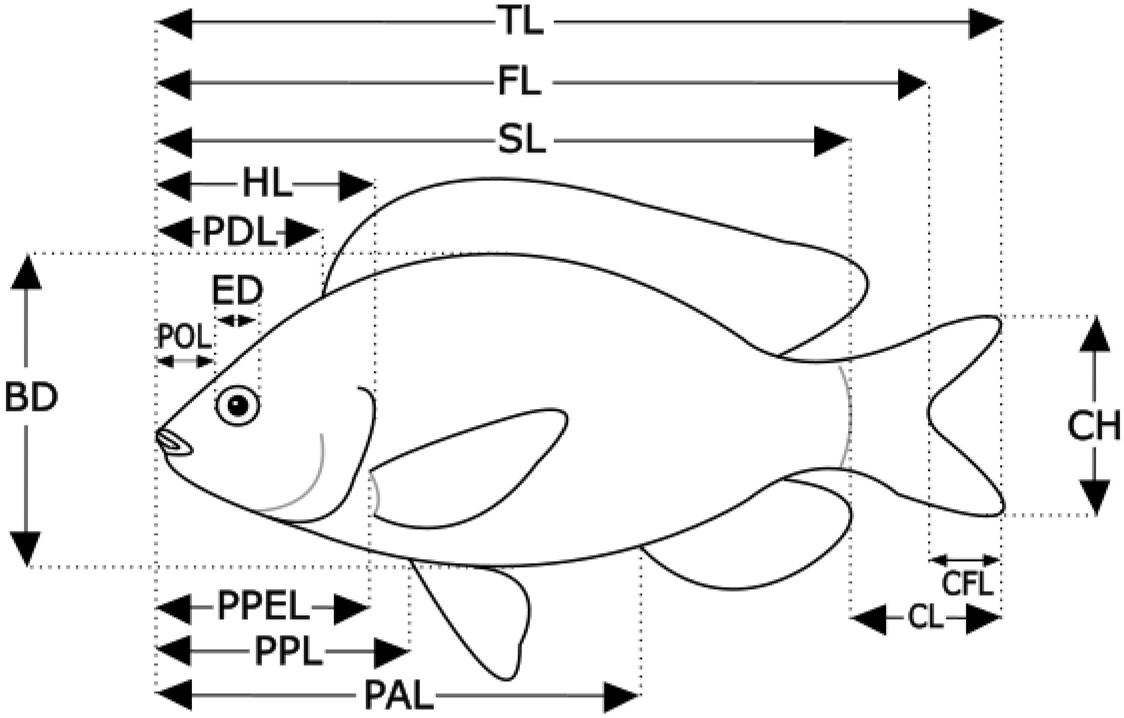

**Figure 2** Lateral view of a generic reef fish illustrating the morphological measures used in this study, including: total length (TL), measured from the upper lip to the end of the caudal fin; standard length (SL), measured from the upper lip to the caudal fin base of the specimen; head length (HL), measured from the upper lip to the opercula flap; pre-dorsal length (PDL), measured from the upper lip to the base of the first dorsal spine; pre-anal length (PAL), measured from the upper lip to the base of the first anal spine; pre-pelvic fin length (PPL) is measured from the upper lip to the base of the pelvic spine; pre-pectoral length (PPEL) is measured from the upper lip to the base of the pectoral fin; eye diameter (ED) is measured from the diameter of the eye; pre-orbit length (POL) is measured from the upper lip to the rim of the eye; body depth (BD) is measured from the dorsal base to the pelvic fin base; caudal height (CH) is measured from the upper margin of the caudal fin to the lower margin of the caudal fin; caudal length (CL) was measured from the difference between TL and SL; and caudal fork length (CFL) is measured from the difference between TL and FL. If a specimen was missing FL, I examined the image on Fishbase to determine whether a forked tail was present and the measurement was simply missed, or if the CFL measurement was zero because the specimen did not have a forked tail.

### 2.3.3 Gradients of fish species richness and morphological diversity in the South Pacific

Before examining gradients in morphological diversity for fishes in the South Pacific, I first examined if my final data set displayed the expected west-to-east and poleward decline in fish species richness among locations. Quantifying gradients of species richness allowed me to explore correlated changes in species richness and morphological diversity across the seascape, as well as providing an internal check that my data curation procedures produced a data set that reflected scientific consensus for fishes in my area of interest. Trends in morphological diversity for my sample locations, were examined using multivariate dispersions. Multivariate dispersions tend to be less sensitive to differences in species richness and sampling effort than other commonly used measures of morphological diversity. This property of multivariate dispersions was particularly important in my case where there is a known gradient in species richness across my sampled seascape. To calculate multivariate dispersions I first calculated the Euclidean distance matrix of my trait-by-species dataset, then I used the 'betadisper' function in the package vegan (Oksanen *et al.*, 2018) to calculate the median distance to the centroid for each sampled location. Once I had calculated species richness and morphological diversity for my sampled locations, I used a Spearman's rank order correlation to determine the magnitude, orientation and significance of the associations between species richness and morphological diversity for fishes across my study region. Furthermore, to examine associations between species richness and morphological diversity at the family level, I repeated the analysis above for each of the nine families.

### 2.3.4 Analysis of morphological change across latitude and longitude

To examine changes in fish morphology across the seascape I used a redundancy analysis (RDA) implemented in the package vegan. Here, the Euclidean distance matrix of my trait-by-species data was the response and the predictors were latitude and longitude. The significance of the association between each geographic variable and morphological variation was examined by permuting the data 9999 times. To examine morphological change across these large-scale geographical gradients within-families, I repeated the analysis above for each family. Last, to investigate if changes in morphology along the geographic gradients were similar among families, I used a congruence among distance matrices (CADM) approach implemented in the ape R package (Paradis, Claude, & Strimmer, 2004). Here, for each family I calculated the Euclidean distance matrix of the weighted average trait scores for the geographically constrained RDA axes, and examined the congruence among these distance matrices using Kendall's coefficient. The significance of the Kendall coefficient was examined by permutation (9999 permutations).

## 2.4 Results

### 2.4.1 Gradients of fish species richness and morphological diversity in the South Pacific

Species richness for the nine fish families I examined followed the well-known reef fish biodiversity gradient, where highest species richness was found closest to the equator and declined pole-wards. Additionally, I also found evidence for a strong longitudinal decline in species richness where the highest richness was found in western areas nearer the IAA (i.e. Papua New Guinea and North Eastern Australia), and decreased eastwards. The gradient of declining species richness towards the south and east of the South Pacific was consistent among all nine families (appendix 2).

In contrast to species richness, morphological diversity, measured using multivariate dispersions, generally increased toward the south and east, despite mixed results between families (appendix 3). To confirm that this gradient was not driven by gradients in species richness, I rarefied morphological diversity, by repeatedly resampling (1000 resamples) the species lists for each location to only 30 species and calculating multivariate dispersions for the rarefied communities. Although the multivariate dispersions for the observed communities were more precise than for rarefied communities, there was no bias introduced by sample size, indicating that the gradient in morphological diversity that I observed was not driven by differences in species richness.

Despite the overall data showing a negative Spearman's rank correlation ($r$ = -0.494) between species richness and morphological diversity, only two of the nine fish families I examined showed a negative correlation (Scaridae and Pomacentridae) with the remainder displaying largely positive correlations (figure 4). Although the datasets used in the overall analysis and the family-level analysis differed; in the latter case, species and locations were removed from the analysis where there were less than two species representing a family for a given location (e.g. Pomacanthidae in Niue, Easter Island, and Kermadec Islands) there were no obvious outliers or influential samples that could have driven the discordance between the overall and family-level analyses.

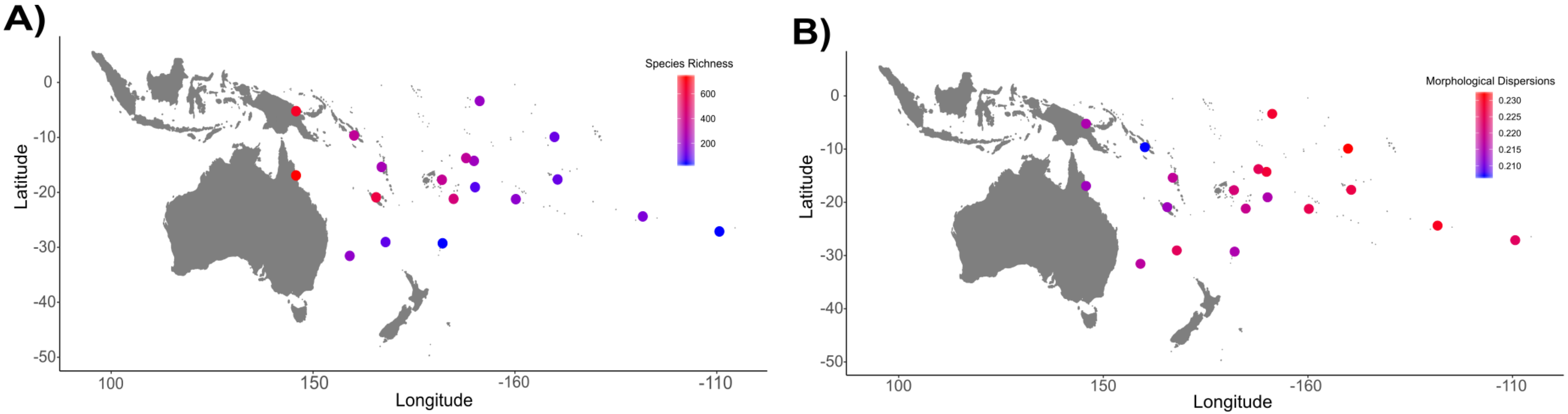

**Figure 3** Species richness (**A**) and morphological diversity (**B**) for each sample location for the nine families considered in my study (Acanthuridae, Apogonidae, Blenniidae, Chaetodontidae, Gobiidae, Labridae, Pomacanthidae, Pomacentridae, Scaridae). Warmer colours indicate higher species richness and higher morphological variation while cooler colours indicate lower species richness and lower morphological variation.

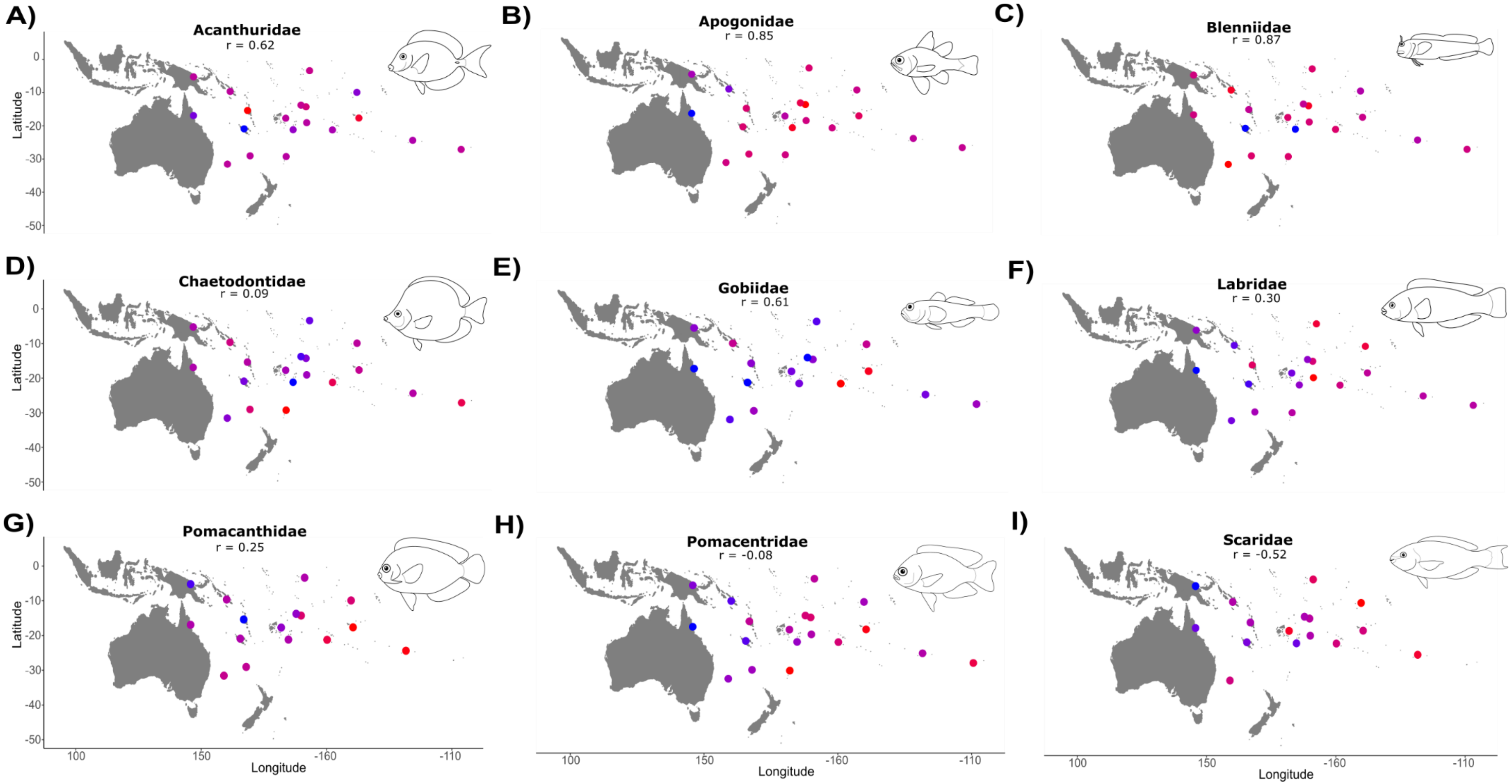

**Figure 4** Rank difference between species richness and morphological diversity for nine reef fish families within the South Pacific: **A**) Acanthuridae, **B**) Apogonidae, **C**) Blenniidae, **D**) Chaetodontidae, **E**) Gobiidae, **F**) Labridae, **G**) Pomacanthidae, **H**) Pomacentridae, **I**) Scaridae. Warm colours indicate low species richness and high morphological diversity, cool colours indicate high species richness and low morphological diversity, and purple colour indicate similar dispersion and species richness ranks.

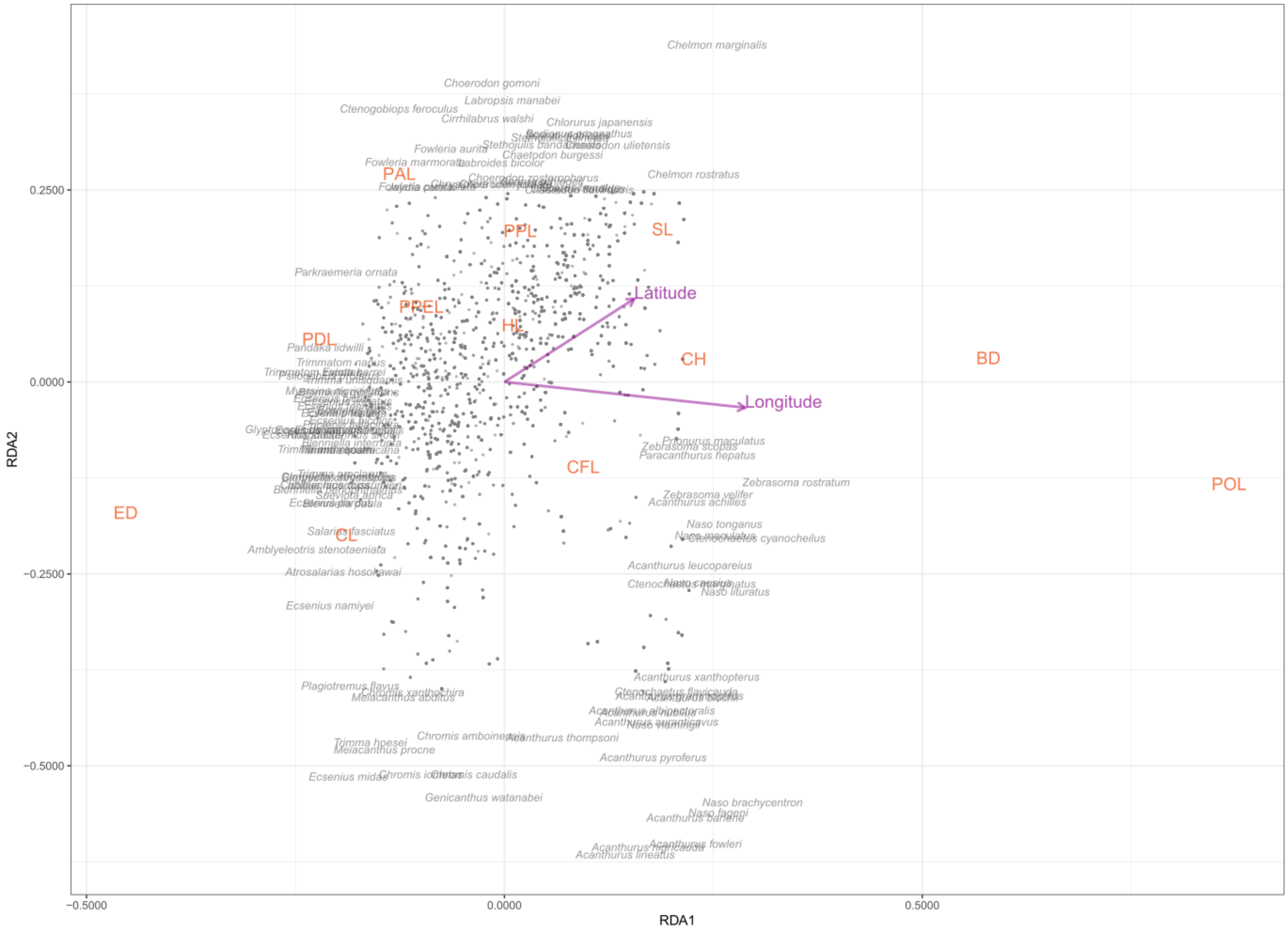

**Figure 5** Redundancy analysis (RDA) with latitude and longitude (arrows) plotted as explanatory variables and the centroids of the 12 standardised morphological traits: standard length (SL), head length (HL), pre-dorsal length (PDL), pre-anal length (PAL), pre-pelvic fin length (PPL), pre-pectoral length (PPEL), eye diameter (ED), pre-orbit length (POL), body depth (BD), caudal height (CH), caudal length (CL), and caudal fork length (CFL). Names display the 3% of the species with the most extreme values for the constrained axes and the points refer to the other 97% of species.

### 2.4.2 Morphological change across latitude and longitude

Across all families, I found evidence for significant variation in the first constrained axis of fish trait variation (RDA1 $P_{(\text{perm})} = 0.0001$) but not the second constrained axis (RDA2 $P_{(\text{perm})} = 0.2381$). Furthermore, I found a significant association between fish trait variation and longitude ($P_{(\text{perm})} = 0.0001$) as well as latitude ($P_{(\text{perm})} = 0.0033$). For RDA1, latitude and longitude were orientated in the same direction, indicating the fishes inhabiting eastern and southern locations in the South Pacific had similar morphology. Specifically, fish inhabiting southern and eastern locations tended to have large preorbital lengths with longer and deeper bodies, while fish inhabiting equatorial and western locations tended to have large eyes, relative to their head lengths.

Examining each family independently, I found geographic gradients in morphology were not consistent (appendix 4). In Labridae, I found evidence for RDA1 ($P_{(\text{perm})} = 0.0147$) and RDA2 ($P_{(\text{perm})} = 0.0113$) as well as evidence for significant association between fish morphological variation and longitude ($P_{(\text{perm})} = 0.0052$) as well as latitude ($P_{(\text{perm})} = 0.0063$). Morphological change along latitude and longitude in Labrids was largely independent with longitude strongly associated with RDA1 and latitude strongly associated with RDA2 indicating that in eastern locations, Labrids had large pre-pelvic and pre-dorsal lengths, whereas in southern locations, Labrids had longer bodies and smaller eyes. Pomacanthidae indicated significant variation along RDA1 ($P_{(\text{perm})} = 0.0029$) but not RDA2 ($P_{(\text{perm})} = 0.9721$) and I only found evidence for an association between morphological variation and longitude ($P_{(\text{perm})} = 0.0071$) but not latitude ($P_{(\text{perm})} = 0.\ 4449$). For Pomacanthidae, I found that fishes inhabiting more easterly locations had greater caudal lengths, caudal fork lengths and eye diameters.

Families with marginally significant morphological variation for RDA1 included: Acanthuridae ($P_{(\text{perm})} = 0.0844$) with trait variation marginally associated to latitude ($P_{(\text{perm})} = 0.0714$); and Blenniidae ($P_{(\text{perm})} = 0.0669$) with trait variation marginally associated to longitude ($P_{(\text{perm})} = 0.0665$). For Blenniidae, eye diameter (relative to head length) decreased with longitude, while for Acanthuridae caudal length, caudal fork length and pre-orbit length (relative to head length) decreased, and body depth increased with latitude. In the remaining fish families, there were no apparent gradients in morphology associated with changes in latitude and longitude.

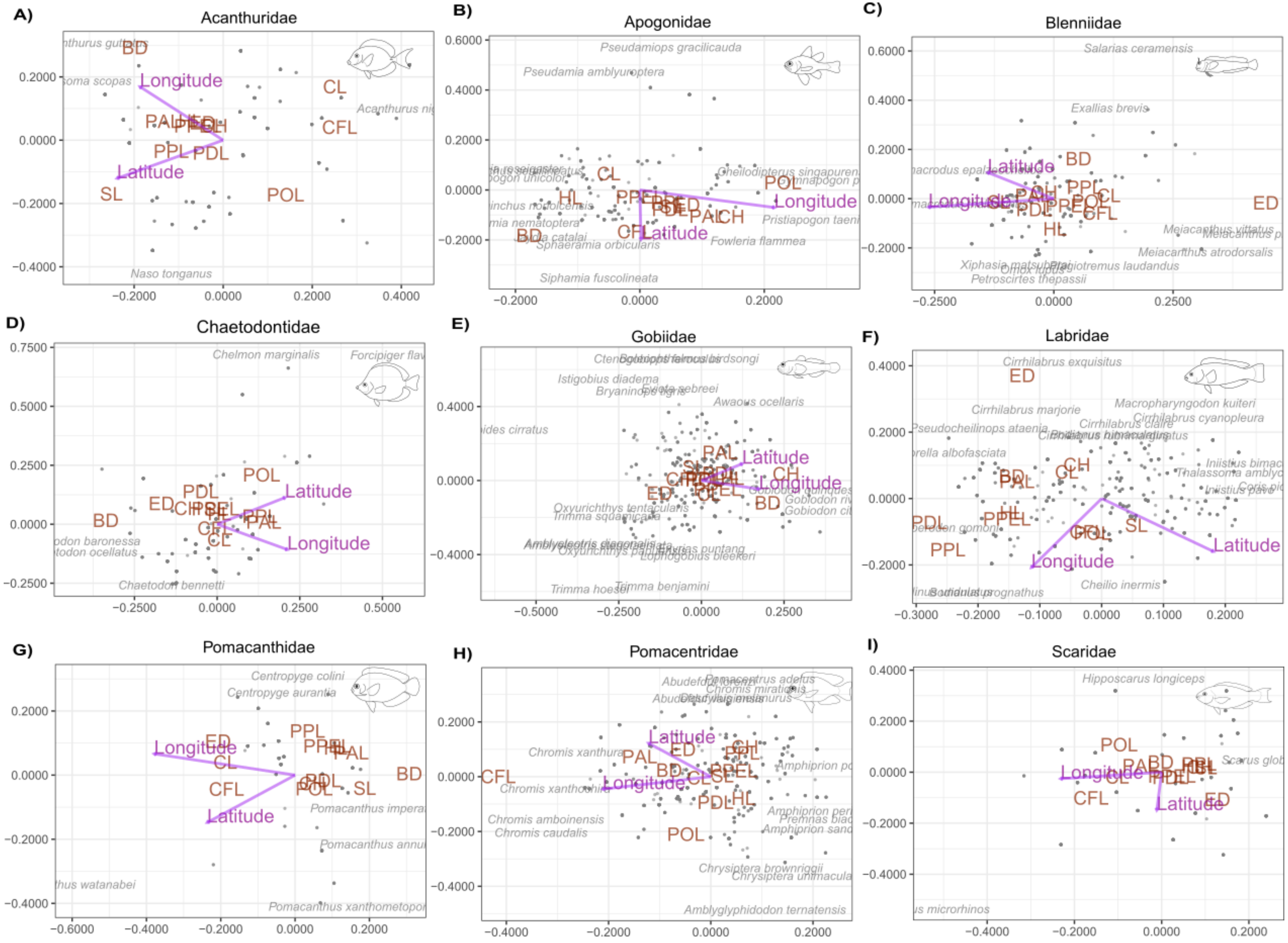

**Figure 6** Redundancy analysis (RDA) for nine reef fish families within the South Pacific: **A**) Acanthuridae, **B**) Apogonidae, **C**) Blenniidae, **D**) Chaetodontidae, **E**) Gobiidae, **F**) Labridae, **G**) Pomacanthidae, **H**) Pomacentridae, **I**) Scaridae; with latitude and longitude (arrows) plotted as explanatory variables and the centroids of the 12 standardised morphological traits: standard length (SL), head length (HL), pre-dorsal length (PDL), pre-anal length (PAL), pre-pelvic fin length (PPL), pre-pectoral length (PPEL), eye diameter (ED), pre-orbit length (POL), body depth (BD), caudal height (CH), caudal length (CL), and caudal fork length (CFL). Names display the top 2% of the species with most extreme morphological traits, while the points refer to the other 98% of the data. For all panels,tropical the x-axis represents the first constrained axis (RDA1) and the Y-axis is the second constrained axis (RDA2

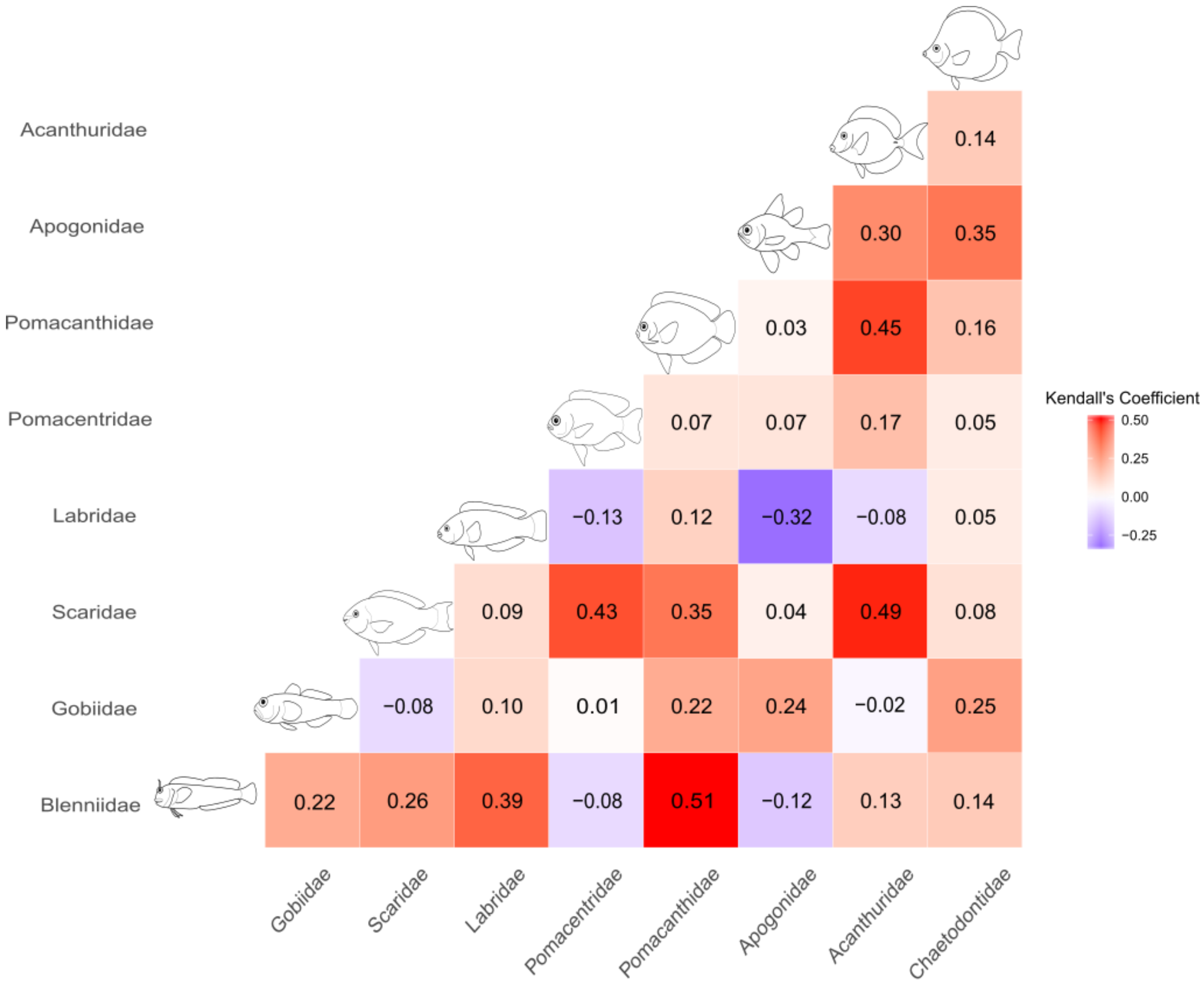

**Figure 7** Congruence of morphological change in response to latitude and longitude for nine common reef fish families within the South Pacific. The values in each box are Kendall's coefficients for the morphological similarity/dissimilarity between taxa. Warm colours indicate similar morphological changes in relation to latitude and longitude, while colder colours indicate an opposing or dissimilar change in morphology in response to latitude and longitude.

I found that overall morphological change in response to latitude and longitude among fish families in the South Pacific, was positive ($w = 0.24$) and significant ($P_{(\text{perm})} = 0.0004$) indicating coordinated changes in morphology. Pomacanthidae and Blenniidae showed the greatest similarity in their morphological change in response to latitude and longitude ($w = 0.51$) followed by Acanthuridae and Scaridae ($w = 0.49$) then Acanthuridae and Pomacanthidae ($w = 0.45$). Conversely morphological change in response to latitude and longitude in Labridae and Apogonidae was negatively correlated ($w = -0.32$), as was in Labridae and Pomacentridae ($w = -0.13$) albeit to a lesser extent.

## 2.5 Discussion

Patterns of species richness across the Pacific Ocean have been described for numerous marine taxa and show a decline in richness toward the poles and the eastern Pacific (Connolly *et al.*, 2003; Edgar *et al.*, 2017; Sanciangco *et al.*, 2013). However, gradients of morphological change within the Pacific seascape are still largely undescribed, though there is some evidence for directional morphological change in response to isolation and environmental variables correlated with latitude (Jacquet *et al.*, 2017; Luiz *et al.*, 2012). Here, I analysed morphological change across the Pacific for nine shallow reef fish families and found that morphological diversity at an assemblage-level displayed an opposite trend to species richness, increasing eastward and poleward across the Pacific. Furthermore, I found that morphological change in reef fishes of the South Pacific was more strongly associated with increasing longitude (from west to east) than increasing latitude. These geographic-morphological changes were coordinated for some families, but not necessarily according to those which share similar body plans or are more phylogenetically related. Overall, my analysis suggests reef fish species within assemblages are more morphologically distinct from each other in high latitude and eastern locations when compared to more species diverse regions at the equator or closer to the IAA.

The strongest responses in both species richness and morphological diversity were in association with longitude, but in opposing directions. As expected, species richness was highest in the western Pacific closest to the IAA, and declined towards the isolated regions in the east (Bellwood *et al.*, 2009). This decline is likely caused by reduced colonisation success and reduced reef area in the more remote islands in the south-eastern Pacific (Barneche, Rezende*, et al.*, 2018; Bellwood & Hughes, 2001). However, despite having fewer species in the east Pacific, these fish assemblages are more morphologically diverse when compared to west Pacific fish assemblages. Presumably, because there are fewer species and thereby less interspecific competition, species in the eastern Pacific can occupy more morphological space as there is more available niche space to fill. For example, specialised herbivorous fishes are common in the tropics where there is intense biotic interactions, whereas colder areas omnivorous fishes are more common as they can occupy more niches and have more resources available (Longo *et al.*, 2018). Therefore, new species that are more morphologically different from the existing community have to potential to fill different niches that may be available, enabling them to persist in these locations.

Despite a consistent decline in species richness both eastward and poleward within each family, patterns of morphological diversity across latitude and longitude varied among families. In contrast to the negative correlation between species richness and morphological diversity found at the assemblage-level, when analysed at the family-level, I found that the correlation between species richness and morphological diversity within families was generally positive. It is possible that species richness-morphological diversity correlations at a family-level may reflect different strategies to reduce competition within each family which are not apparent at an assemblage level. For instance, Blenniidae, which displayed the largest correlation ($r = 0.873$) between species richness and morphological diversity of all nine families, consume a variety of diet items (Brandl *et al.*, 2018) while Scaridae, with their modified jaws and fused teeth, have a more specific niche within reef ecosystems (Gobalet, 2018) and displayed a negative correlation ($r = -0.523$). This negative species richness-morphological diversity correlation may be indicative of the species niche being heavily constrained in areas of high coral abundance, where they compete with confamilial species (Muñoz, Motta, & Ross, 2000). In contrast, at higher latitudes and more isolated environments within the South Pacific, competition may be more relaxed, and resources may differ (Harmelin-Vivien, 2002), enabling greater relative morphological diversification of the Scaridae species.

At an assemblage level, I found evidence for coordinated changes in morphology across both longitude and latitude. In particular, fishes had deeper and longer bodies in the eastern Pacific, and to a lesser extent in the southern Pacific (figure 5), supporting general increases in body size with increasing latitudes and increasing isolation (Barneche, Rezende*, et al.*, 2018; Luiz *et al.*, 2012). Because isolated reefs have a lower species richness, larger fish are thought to benefit from being able to exploit more varied food resources (Jacquet *et al.*, 2017). Additionally, with mortality disproportionally higher among new recruits (Almany & Webster, 2005; Sale *et al.*, 1984), larger species benefit with faster growth rates (Shima & Findlay, 2002) and a deep bodies reduce predation from gape-limited fishes (Hodge *et al.*, 2018; Nilsson & Brönmark, 2000). However, although not significant, Pomacanthids and Chaetodontids had smaller body depths in the east Pacific. Both the Pomacanthids and Chaetodontids generally have a disc shaped body, a reduced body depth may create a more streamlined shape to increase movement speed for predator escape (Floeter *et al.*, 2018). Furthermore, Pomacanthids as well as Pomacentrids and Scarids, although not significant, also had longer caudal fins and caudal fork lengths toward the east and south, traits often associated with greater swimming speed and acceleration in fishes (Blake, 2004).

A less renowned morphological change that I observed across the nine fish families I examined was an increase in pre-orbital length relative to head length in response to both latitude and longitude. Presumably, the relative length of the pre-orbital region is related to the length of the jaw, and thereby gape size. As diversity and abundance of fishes declines moving east and south, a larger gape would increase the diversity of prey species or food items a fish could consume, and may improve predation success (Goatley & Bellwood, 2009). Concurrent changes in jaw morphology and declining species richness have been documented for a diverse community of bony-fishes distributed along a 2000m depth gradient in the south-western Pacific, where species are presumed to become more generalist at greater depths due to depleted feeding opportunities (Myers *et al.*, 2019). Although the change in relative pre-orbital length in response to latitude and longitude was significant at the assemblage level, the trends differed for the individual families. For instance, the pre-orbital length of blennies and gobies did not change across latitude and longitude and could be a consequence of more constrained morphology. While the reduction of pre-orbit length in Pomacanthidae and Acanthuridae may be the result of different feeding modes in high latitudes and eastern locations. For example, smaller mouths can be beneficial for precise feeding on zooplankton and benthic invertebrates when paired with larger eyes for acuity (Goatley & Bellwood, 2009).

Contrary to previous studies, I found a general decrease in eye size relative to head length with increasing latitude (Myers *et al.*, 2019). Furthermore, this decrease in eye diameter relative to head length was also evident across longitude for many of the fish families despite no expected change in the light environment toward the eastern Pacific. Therefore, my results indicate this decrease in eye diameter is due to the relationship with other morphological measurements that affect head length. For instance, increasing pre-orbit length would cause a direct increase in head length and cause the eyes to appear relatively small, even if absolute eye size was to remain constant. Furthermore, if fishes are becoming overall larger and the increase in size for the head and body were consistent then changes in head length would be obscured. Indeed, for some families there was no strong association of pre-orbital length with latitude and the expected relationship of increasing eye diameter with increasing latitude was recovered (Acanthuridae and Pomacanthidae).

Among my nine families, similar morphological changes in response to latitude and longitude were found among families that shared functional roles and niche requirements in some cases. For instance, Blenniidae and Labridae both had decreased eye diameter with increasing longitude. Both taxa are known to have a variable diet comprised of algae, plankton and microinvertebrates (Floeter *et al.*, 2018; Goatley & Bellwood, 2009; Kotrschal & Thomson, 1986; Westneat *et al.*, 2005), moving eastwards coral reef area and productivity decreases likely causing a reduction in possible prey items. For example, Blenniidae in eastern communities may be filling benthic detritivore roles and Labridae filling herbivorous niches where larger eye sizes may have little advantage (Goatley & Bellwood, 2009). Conversely, Pomacanthidae have a varied diet including algae, sponges, and benthic invertebrates (Bellwood, van Herwerden, & Konow, 2004). Increases in eye diameter in eastern locations may indicate a diet shift towards smaller or more mobile invertebrates where larger eyes may allow for more precise capture (Goatley & Bellwood, 2009; Goatley, Bellwood, & Bellwood, 2010). Nevertheless, particular morphological characteristics such as eye diameter increasing or decreasing eastward and poleward may reflect a trade-off with pre-orbital length (as a proxy for gape size, as explained above). In particular, predators, and especially piscivores, pre-orbit length may contribute a large portion of head length, whereas in other functional groups, eye size relative to head length is more important for particular feeding modes. Regardless, the converging of the morphological traits may be indicative of shift in niche space, where converging traits may be the result of limited niche space.

In several cases, families that had correlated morphological change in response to latitude and longitude were not similar in body plan, niche, and were not closely related phylogentically. For instance, Pomacanthidae and Blenniidae demonstrated the highest similarity ($w$ = 0.51) in morphological change despite these families having different general body shapes and occupying different functional roles. The similar morphological changes in both families suggest they may be responding to the same environmental changes across the Pacific. In particular, the reduction of primary production in higher latitude regions due to a reduced light may lead to converging feeding strategies from limited dietary options. Acanthuridae and Pomacanthidae also displayed coordinated morphological changes ($w$ = 0.45), however, both these families are known to have a similarly deep body shapes, and so their coordinated changes may be less surprising. For example, the reduced body depth in Pomacanthidae along latitude and longitude may be a response to a reduction in coral habitat and therefore fewer refuges, where the taxa require a streamlined body shape for increased swimming speed in order to escape predators (Floeter *et al.*, 2018). In contrast, Labridae and Apogonidae demonstrated opposing morphological change ($w$ = -0.32), suggesting these families are adopting different approaches to surviving within the South Pacific Ocean.

Despite gathering and analysing over 5130 records of fishes across 19 locations in some of the most diverse reefs in the Southern Pacific, several caveats in this dataset need to be recognised. First, for many species, morphological measurements were missing or unreliable, therefore although data missingness was low and relatively consistent (<22.1% among locations), it is possible that the morphology of these missing species may influence the patterns I present. Second, although I compared changes in 12 different morphological traits, important ecomorphological trait measurements such as mouth gape size were not available. Without any measurements relating to the gape size I could only presume increases in pre-orbit length relative to head length would correlate with mouth size. Having measures of mouth size would have allowed us to more robustly infer dietary changes across latitude and longitude. Last, the same morphological measurements for each species were used at every location where the species occurred, thereby ignoring intraspecific morphological variation that would naturally occur across the species ranges. Despite everything mentioned, my analysis provided insight into large scale richness patterns coordinated among families with a general correlation to morphological diversity, furthermore, similar morphological changes corresponded to gradients was identified among families within the South Pacific Ocean.

In summary, my findings provide a first look into both the morphological diversity and geographic changes in morphology for reef fishes across the Pacific Ocean. Surprisingly, I found longitude more strongly influenced morphological diversity and change, despite the numerous environmental factors correlated with latitude. Presumably, isolated islands in the east are difficult for all reef fish species to colonise and survive in, resulting in the strong filtering of species. Such a phenomena has been well described to impact levels of species richness across the Pacific. my analysis of the morphology of these species confirms the importance of body size in colonising the eastern Pacific. However, my analysis provokes further investigation into environmental drivers of biodiversity patterns and morphological change across the Pacific and deeper examination of the factors causing divergent changes among families.  As our climate changes and ocean barriers are eroded, it will be interesting to witness whether these trends in species richness and morphological diversity across the Pacific persist.

# Chapter 3: Temporal changes in the morphology and biogeographic affinities of fish assemblages at Rangitāhua

## 3.1 Abstract

Documenting temporal changes in community composition is challenging, particularly for rarely visited locations where baselines for biodiversity have not been formally established. Rangitāhua, or the Kermadec archipelago, is a relatively young and pristine group of oceanic islands in the Southwest Pacific Ocean and one of the most remote and isolated archipelagos on the planet. Accordingly, with each research expedition, the species list for reef fishes resident around the islands increases. These new species records at Rangitāhua may be due to increased sampling effort over time, however there may also be an influence of climate change leading to the arrival of more tropical species as they extend their ranges into subtropical locations such as Rangitāhua. Here, I assessed whether Rangitāhua was undergoing tropicalisation, where I expected that the reef fishes recently colonising the islands would be coming from more tropical regions, and that morphological variation in the fish assemblage would also change as environmental conditions becomes more tropical. Using a list of 149 shallow reef Teleost fishes including their dates of first sighting at Rangitāhua (1984 – 2017), I investigated the contribution of different geographic regions to Rangitāhua's reef fish assemblage to identify any temporal change in the biogeographic affinities of the species assemblage. Additionally, I inferred whether fishes with more tropical affinities are rare at the high-latitude island (indicative of being recent colonisers or not yet established), and whether there has been a change in morphological variation of the fish assemblage as new species colonise. I identified a temporal shift in the biogeographic affinities of the Rangitāhua fish assemblage with an increasing contribution from tropical regions. Newly discovered, more topical species, only occurred in low numbers, possibly because they are still in the early colonising stage or because the island's environment is still more temperate than these fish require to increase in abundance significantly. I also found evidence for temporal changes in the morphology of the fish assemblage at Rangitāhua, however this did not suggest a change from a more 'temperate' to a more 'tropical' morphology. It is possible that the tropical species that have recently colonised Rangitāhua display a temperate-like morphology, allowing them to more easily survive in the high-latitude environment at Rangitāhua. Overall, this study describes a temporal shift in the biogeographic affinities of Rangitāhua's Teleost fish assemblages, indicative of increased colonisation by species of tropical origin, or increased discovery of tropical species at the islands and may serve as an early warning signal for climate driven shifts.

## 3.2 Introduction

The biodiversity of a region naturally changes through time as species accumulate, speciate and go extinct. However, climatic changes over the last few decades have accelerated the rate and type of biodiversity change (Burrows *et al.*, 2011). Historically, low latitude regions have been considered 'centres of biodiversity', with theories describing an increased speciation rate (Cowman & Bellwood, 2013; Rohde, 1992) and reduced extinction rate (Bellwood *et al.*, 2009; Cowman & Bellwood, 2013; Cowman *et al.*, 2017). As temperatures rise, predominantly tropical species, residing at low latitudes are expected to shift their ranges into higher, temperate latitudes, changing the biodiversity of source and recipient regions (García Molinos *et al.*, 2015). The tropicalisation of higher latitudes has been observed in several regions, sometimes with drastic consequences on the recipient ecosystems (Pecl *et al.*, 2017; Sorte, Williams, & Carlton, 2010). In particular, for marine coastal ecosystems, poleward range shifts have been observed to be considerably faster than in terrestrial ecosystems despite oceans warming slower than the land (Burrows *et al.*, 2011; Poloczanska *et al.*, 2013). Range shifts are important indicators of potential biodiversity and ecosystem change; however, the detection of a range shift or a biodiversity change requires an initial understanding of the regional biodiversity, natural rates of species accumulation, and types of change through time which may not always be readily available.

Oceanic islands have played a central role in establishing general rules regarding expected rates and types of species accumulation and biodiversity change through time (MacArthur & Wilson, 1967; Warren *et al.*, 2015). Because oceanic islands have never been attached to continents, much of their biodiversity depends on the dispersal of species from elsewhere. Therefore, the biodiversity found on islands is often closely related to the biodiversity of the nearest geographical location (Drew & Amatangelo, 2017), and the older and larger the oceanic island, the more species the island tends to have (Hachich *et al.*, 2015; Lomolino, 2000). Furthermore, the species that colonise islands often have traits that confer high dispersal ability (Barneche, Rezende*, et al.*, 2018; Barneche, Robertson*, et al.*, 2018; Jenkins *et al.*, 2007; Luiz *et al.*, 2015) or increase their potential to establish in the often depauperate island communities, particularly during the early stages of biodiversity accumulation in island systems (Luiz *et al.*, 2013; Luiz *et al.*, 2012). Conventional wisdom also dictates that the biodiversity found within an oceanic island will be shaped by the environmental conditions and available niche space (Barneche, Rezende*, et al.*, 2018; Burt *et al.*, 2011); the biodiversity of the island will be more similar to environmentally similar source locations than environmentally dissimilar source locations (Burt *et al.*, 2011). As a result, each oceanic island have a unique range of species, depending on the proximity of available source locations, its age, and it's environmental setting (Hachich *et al.*, 2015). However, given that climate change is likely to alter both the potential source locations and the environmental setting of oceanic islands, potential coordinated change may occur in the rate and type of species accumulating on oceanic islands. Depending on the availability of source locations and dispersal vectors, naturally depauperate high latitude oceanic islands may become more biodiverse and tropicalised.

Under a scenario of tropicalisation, where species are potentially arriving from different source locations and the environmental settings of high latitude oceanic islands are changing, the morphological diversity of the island assemblage may also be expected to change. For reef fishes, several morphological traits are known to be associated with species found around isolated island reef systems (Barneche, Rezende*, et al.*, 2018; Bender *et al.*, 2013; Jacquet *et al.*, 2017; Luiz *et al.*, 2013), and some are known to change across latitude (Luiz *et al.*, 2012). For instance, isolated islands are known to have a higher proportion of large bodied fish when compared to continental locations (Jacquet *et al.*, 2017). Furthermore, the temperature-size rule (Atkinson, 1994; Ray, 1960) describes ectotherms having larger body sizes with higher latitudes due to slower maturation rates in colder temperatures (Blanck & Lamouroux, 2007; Kingsolver & Huey, 2008; van Rijn *et al.*, 2017). Additionally, body size assists in island colonisation with dispersal and persistence by improved fecundity, increasing the potential variety of prey items, reducing the likelihood of predations, and increasing territory spaces (Barneche, Robertson*, et al.*, 2018; Bender *et al.*, 2013; Jacquet *et al.*, 2017; Luiz *et al.*, 2013). For instance, reef fishes in the South Pacific tend to conform to the temperature-size rule with increased body size in higher latitudes, and increasing with longitude, presumably to assist the colonisation process with isolation increasing eastwards (Chapter two). Morphological diversity is known to vary across large scales with traits linked to the functional ability of species to survive within particular habitats. Therefore, as more tropical species, and species from different source locations shift their distribution into high-latitude oceanic islands, the morphological variation on the reef fish assemblages is likely to change.

Within the South Pacific exist numerous isolated oceanic islands. In general, the species richness of reef fishes in the South Pacific declines toward the poles and into the East Pacific (Chapter two). Rangitāhua, or the Kermadec Islands, is one of the highest latitude, and most isolated islands of the Pacific. Even considering their geographic setting, Rangitāhua is very depauperate in reef fishes and corals (Schiel, Kingsford, & Choat, 1986), possibly owing to their relatively young age; estimated to be around 0.5 million years old (Latter *et al.*, 1992). The reef fish assemblage of Rangitāhua includes species of temperate and tropical origin, with affinities to the New Zealand mainland, the far east Pacific and the Tasman sea islands to the west (Norfolk Island

and Lord Howe Island), as well as a collection of broadly distributed Indo-Pacific species (Francis, 1991, 1993; Francis & Duffy, 2015; Francis, Grace, & Paulin, 1987). The understanding of the fish fauna surrounding Rangitāhua increases with each expedition to this uninhabited island group, with many recent surveys describing new records of species that occur in very low abundance (Francis & Duffy, 2015). Although the influence of increasing survey effort over time cannot be discounted, the prevalence of new species records and species of low abundance coupled with Rangitāhua's low species richness and levels of endemism, suggests the islands are still actively being colonised. Additionally, it is possible there is a changing colonisation regime, whereby more tropical species are starting to become more common on these high-latitude island reefs.

Here, I use a reef fish species list for Rangitāhua, stratified through time by species' first observation, to evaluate whether there has been a change in the reef fish biodiversity as a result of climate induced species redistributions. I test whether there is an increasing contribution from tropical biogeographic regions over time and with it, a change in the morphology of the reef fish assemblage. First, I expect the relative contribution of tropical biogeographic regions to increase through time; and second, a change in morphology of the reef fish assemblage indicative of different dispersal, colonisation and niche traits changing in importance. Third, if rarity is indicative of recent colonisation, I expect that the contribution of rare species to overall biodiversity will increase over time. Furthermore, I expect that rare species will have more tropical biogeographic affinity than abundant species, and will differ in morphological traits from common species. In contrast, if the increasing discovery of new species records and rare species at Rangitāhua through time is indicative of increased survey effort, I expect no change in relative contribution of biogeographic regions through time and no change in the fish assemblage morphology over time.

## 3.3 Methods

### 3.3.1 Fish species lists of Rangitāhua

Using Francis (2019) and Liggins et al. (2020), I compiled a list of shallow (<50m depth) Teleost fishes found within 1km of the islands of Rangitāhua. From an initial list of 187 species, I retained taxa that possessed typical and comparable morphological features (see below). For instance, seahorses have no caudal fin, and flounders have an extremely specialised morphology that I considered atypical *a priori*.

I then used Duffy and Ahyong (2015), Francis (2019), and Liggins et al. (2020) to determine the earliest recorded date for each species in the fish species list. Figure 1 shows that the accumulation of species has rapidly increasing over the past decades, particularly since the first major fish expedition in 1987. Specifically, during the 1980's, 1990's and 2010's there were large increases in the knowledge of fishes for this region (66 fishes recorded in 1980-1990, 38 fishes recorded in 1990-2000 and 45 fishes recorded in 2010-2017). These three decades of sampling contributed 94.9% of the new species records in my database, so I focused temporal analyses, only on fishes recorded during these three decades. My final list comprised 149 species from 51 families.

In my analyses of temporal changes in fish morphology, species were categorised by the decade of first observation at Rangitāhua. I chose to partition my data in this way rather than focus on the cumulative species list as I only have data representing the first observations of these species and could not be confident that all species present in a previous decade were still present at the islands, i.e. I have no exhaustive data on local species extinctions. However, additional analyses of the cumulative species list where the species list were nested within each time slot (eg, 1989 and earlier, 1999 and earlier, 2010 and earlier) showed similar patterns.

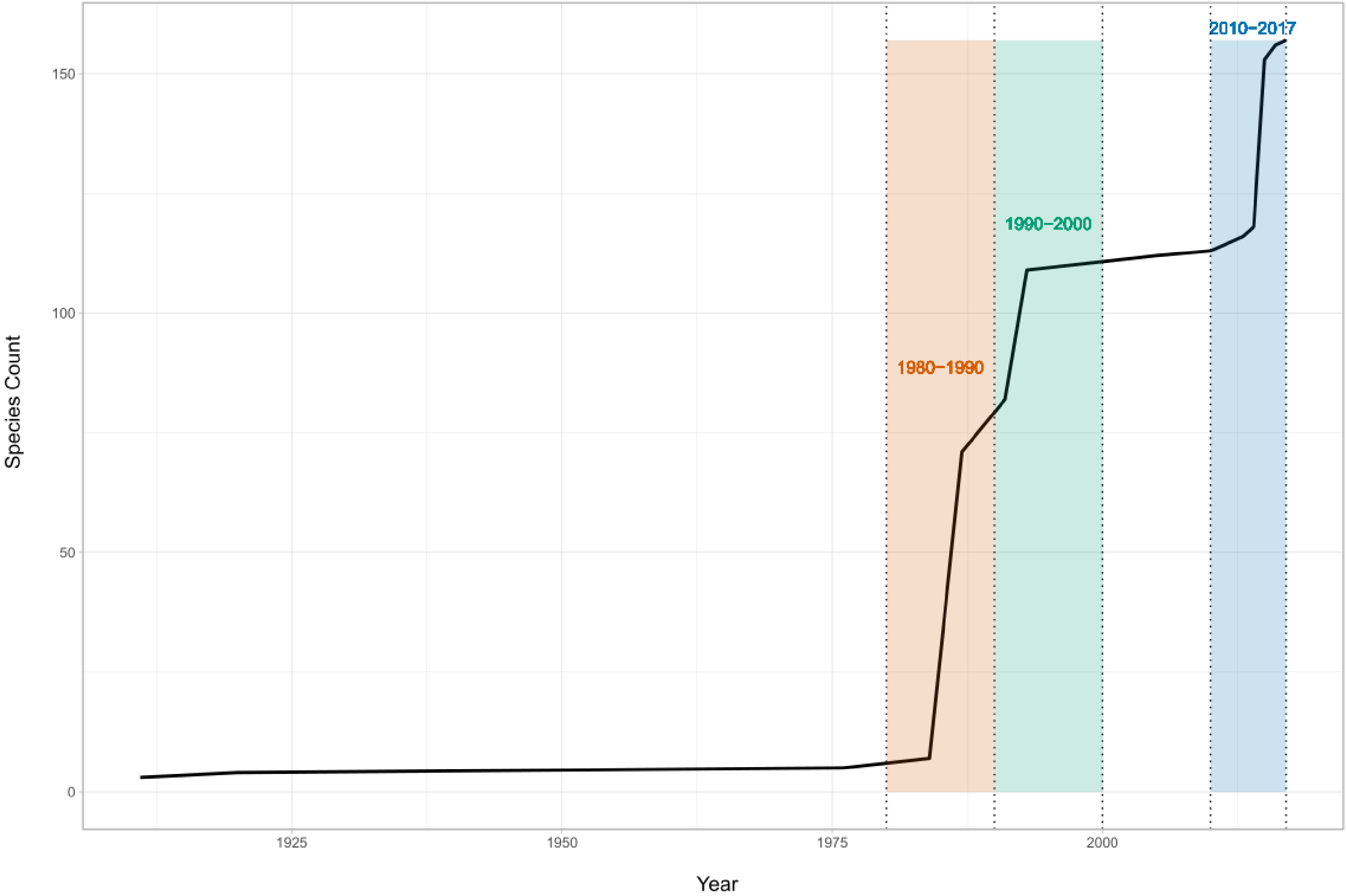

**Figure 1** Accumulation of shallow reef fish species at Rangitāhua from 1911 to 2017. Shaded regions indicate the three decades (1980-1990, 1990-2000, and 2010-2017) that contributed the most species (94.9%) to the Rangitāhua shallow reef fish database.

### 3.3.2 Contribution of biogeographic regions

To characterise the distribution and geographic affinity of each species, I queried the Ocean Biogeographic Information System (OBIS, 2019) database using the 'occurrence' function of the R package Robis (Provoost *et al.*, 2017). This provided all the recorded occurrence records for the species in my species list, except *Flexor incus*, likely due to the recency of its species description.

Although all species on my list are known to occur at Rangitāhua this was not reflected for all species in their OBIS records, accordingly I added the coordinates for Raoul Island (29.27°S, 177.93°W) to each species to ensure their distribution included Rangitāhua. To determine biogeographic contributions to Rangitāhua's fish fauna, I generated a presence/absence matrix where the rows were the fish species of Rangitāhua and the columns were the ecoregions defined in the Marine Ecoregions of the World (MEoW) (Spalding *et al.*, 2007). Although fish specific bioregionalisations are available (Briggs & Bowen, 2012; Kulbicki *et al.*, 2013), I chose to use the MEoW because of their applicability to reef ecosystems in general. I then performed a similarity profile analysis (Clarke, Somerfield, & Gorley, 2008) using the 'simprof' function in the R library clustsig (Whitaker & Christman, 2014) to objectively categorise species into groups with similar geographic distributions. The simprof procedure uses resampling (9999 times) to determine the number of species geographical clusters under a *priori* assumption that there are no clusters. The distance measure I used was the Jaccard's dissimilarity between samples (i.e. species) because of its intuitive interpretation as the proportion of geographic regions two species do not have in common. At an alpha value of 0.05 and 0.01 I found there were 39 and 36 significant clusters respectively, and many clusters with only a single species. Accordingly, I lowered the threshold of significance to 0.001 yielding 32 significant clusters with fewer singleton clusters, allowing for useful inferences to be drawn from my data.

### 3.3.3 Abundance of fish species

To calculate abundance scores, I classify fish species occurring at Rangitāhua as "common", "patchy" or "rare" using survey data for fishes at Rangitāhua, namely: Eddy (2011), Liggins et al. (2020), and Reef Life Survey (Edgar & Stuart-Smith, 2014; Edgar & Stuart-Smith, 2019). Despite each survey occurring around the northernmost island of Rangitāhua (Raoul Island) – different methods were used for each survey, and so I calculated the abundance scores of each species for each survey method independently. First, for each survey, I calculated the weighted mean abundance of each species, where the weighting was the proportion of sampling units (i.e. transects or stations) in which a species occurred. I then calculated the empirical cumulative density function of the weighted mean abundances for each survey. I considered species below the 70th percentile of the cumulative density function for the abundance scores to be “patchy”, species contributing to the top 30th percentile of the cumulative density function for the abundance scores were considered “common” (appendix 5). Last, species known to occur at Rangitāhua (Francis, 2019), but not recorded in *situ* surveys were considered “rare”. Although species abundance scores among survey methods were highly consistent, when species abundance scores were not consistent, I assigned species to the highest (i.e. more common) category score.

### 3.3.4 Morphology of fish species

To explore temporal changes in the morphology of the shallow reef fish community around Rangitāhua, I used the morphometrics function in Rfishbase R package (Boettiger *et al.*, 2012) to extract morphological information for each species in my list. Morphological measures provided by Fishbase (Froese & Pauly, 2019) include the commonly measured features of fishes used for taxonomic inference, for inferences of ecomorphology, and have relevance to several fish functional traits. I elected to include 11 measurements that were able to be measured across the diverse body plans of the fishes included in my species list (figure 2). Where measures were available for more than one specimen per species, I used measures from the largest available specimen in order to avoid the influence of varying ontogenetic stages being used across species. For species with absent morphological measures on Fishbase, or species with measurements based on hand-drawn images (with the exception of *Chelon melinoptera* – known to be drawn to scale from a specimen), specimen images from the fishes of New Zealand book (Roberts, Stewart, & Struthers, 2015) were scanned and the 11 standard measurements were collected. Alternatively, where measurements or photos were not available from these sources, I used photographs from: Atlas of living Australia, the Te Papa Museum collections, and Bold systems to obtain images for measurement. Furthermore, for three species (*Flexor incus, Eviota kermadecensis, Ennaepterygium kermadecensis*) where photographs were, either not available or were imaged poorly, I photographed preserved specimens held at the Auckland Museum. All images gathered were measured with ImageJ (Schneider, Rasband, & Eliceiri, 2012) using a landmark based approach to attain linear measurements (figure 2).

Linear morphological measures were transformed into proportions so that the influence of specimen and species size were minimised, in favour of understanding relative shape changes of fishes. Specifically, head measures (eye diameter (ED) and pre-orbit length (POL)) were proportioned to head length (HL) and body traits (standard length (SL), head diameter (HD), pre-anal length (PAL), pre-dorsal length (PDL), pre-pectoral fin length (PPEL), body depth (BD), caudal height (CH), caudal length (CL), caudal fork length (CFL)) to total length (TL). Although, some studies have used SL rather than TL to standardise body measures, there are unclear guidelines for measuring SL (Howe, 2002) and studies have shown that measurements of TL have significantly lower average error than SL (Önsoy, Filiz, & Bilge, 2011). Other measurements such as pre-pelvic fin length was available, but some of the fish families included in my dataset have no pelvic fins, accordingly I chose to remove pre-pelvic length measurements from my analyses to ensure a greater sample size of species.

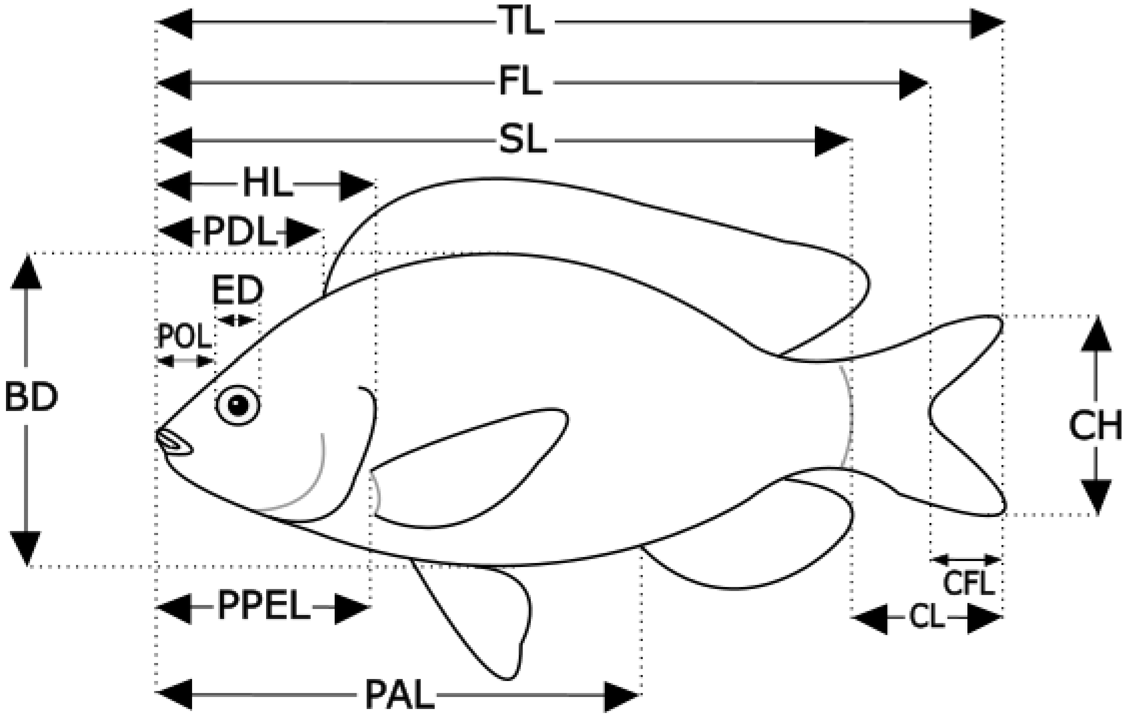

**Figure 2** Lateral view of a reef fish illustrating the morphological measures used in this study, including: total length (TL) is taken from the upper lip to the end of the caudal fin; standard length (SL) is taken from the upper lip to the caudal fin base of the specimen; head length (HL) is from the upper lip to the opercula flap; pre-dorsal length (PDL) is measured from the upper lip to the base of the first dorsal spine; pre-anal length (PAL) is measured from the upper lip to the base of the first anal spine; pre-pectoral length (PPEL) is measured from the upper lip to the base of the pectoral fin; eye diameter (ED) is the diameter of the eye; pre-orbit length (POL) is measured from the upper lip to the eye; body depth (BD) is taken from the dorsal base to the pelvic fin base; caudal height (CH) is the depth of the caudal base; caudal length (CL) was the difference between TL and SL; and caudal fork length (CFL) is the difference between TL and FL. If a specimen was missing FL, I examined the image used for measurement on Fishbase to determine whether a forked tail was present and the measurement was simply missed, or if the CFL measurement was zero (i.e. the specimen did not have a forked tail).

### 3.3.5 Redundancy analysis

To examine temporal changes in fish morphology at Rangitāhua I used a redundancy analysis (RDA) from the package vegan (Oksanen *et al.*, 2018) for R v 3.6.0. Here, the Euclidean distance matrix of my trait by species data was the response and the predictors were decade with three levels (1980's, 1990's and 2010's) and abundance also with three levels (rare, patchy and common). The significance of the association between morphological variation, abundance and the three decades was examined by permutation (9999 permutations).

## 3.4 Results

### 3.4.1 Contribution of biogeographic regions

Examining the distribution patterns of the 149 species in my Rangitāhua species list, I identified 32 significant clusters representing groups of species with similar geographic distributions. The proportional representation of different species groups was used to examine the temporal changes in relative contribution of different biogeographic regions to Rangitāhua's fish fauna. Figure 3B shows the three most highly represented clusters in the 1980's. Species recorded in the 1980's had distributions encompassing higher latitude regions like temperate New Zealand, Southern Australia and the Islands of the Tasman Sea (figure 3B). Species categorised as belonging to cluster 4 and 9 still contribute the most species to the shallow reef community in 2010's, however, species from cluster 8 are no longer as numerically dominant as species from cluster 22, species with Pacific and Indo-Pacific geographic affinities have increased in frequency (figure 3C). The biogeographic clusters that have shown the greatest change in their representation within the fish community of Rangitāhua are clusters 1, 15, 22 which are characterised as species with North Australian, South East Asian, East African, and tropical Pacific geographic affinities (figure 3D).

### 3.4.2 Abundance of fish species

From the overall species list, based on the survey data, 25 species were classified as common, 31 as patchy, and 93 as rare. The majority of fish species classified as common were recorded between 1980 and 1990, and there were no species first observed between 2010 and 2017 that were classified as common. Similarly, patchy species followed the same decline in records over time. However, rare species showed an increase over time, with the vast majority being first observed between 2010 and 2017.

### 3.4.3 Morphology of fish species through time and abundance classes

Using RDA I found a gradient in fish morphology with fishes that have deeper bodies, longer forked tails and shorter pre orbital and pre dorsal lengths at one extreme and fishes that were more slender with shorter tails and longer pre orbital lengths at the other extreme (RDA1: $P_{(\text{perm})} = 0.047$). I also found a significant association between fish morphological variation and decade ($P_{(\text{perm})} = 0.017$) and abundance ($P_{(\text{perm})} = 0.030$). Deeper bodies were more frequent for fishes recorded for the first time in the 1980's and 2010's and for the common fishes. Whereas, newly recorded fishes in the 1990's were more slender and elongated (PDL, POL, PAL).

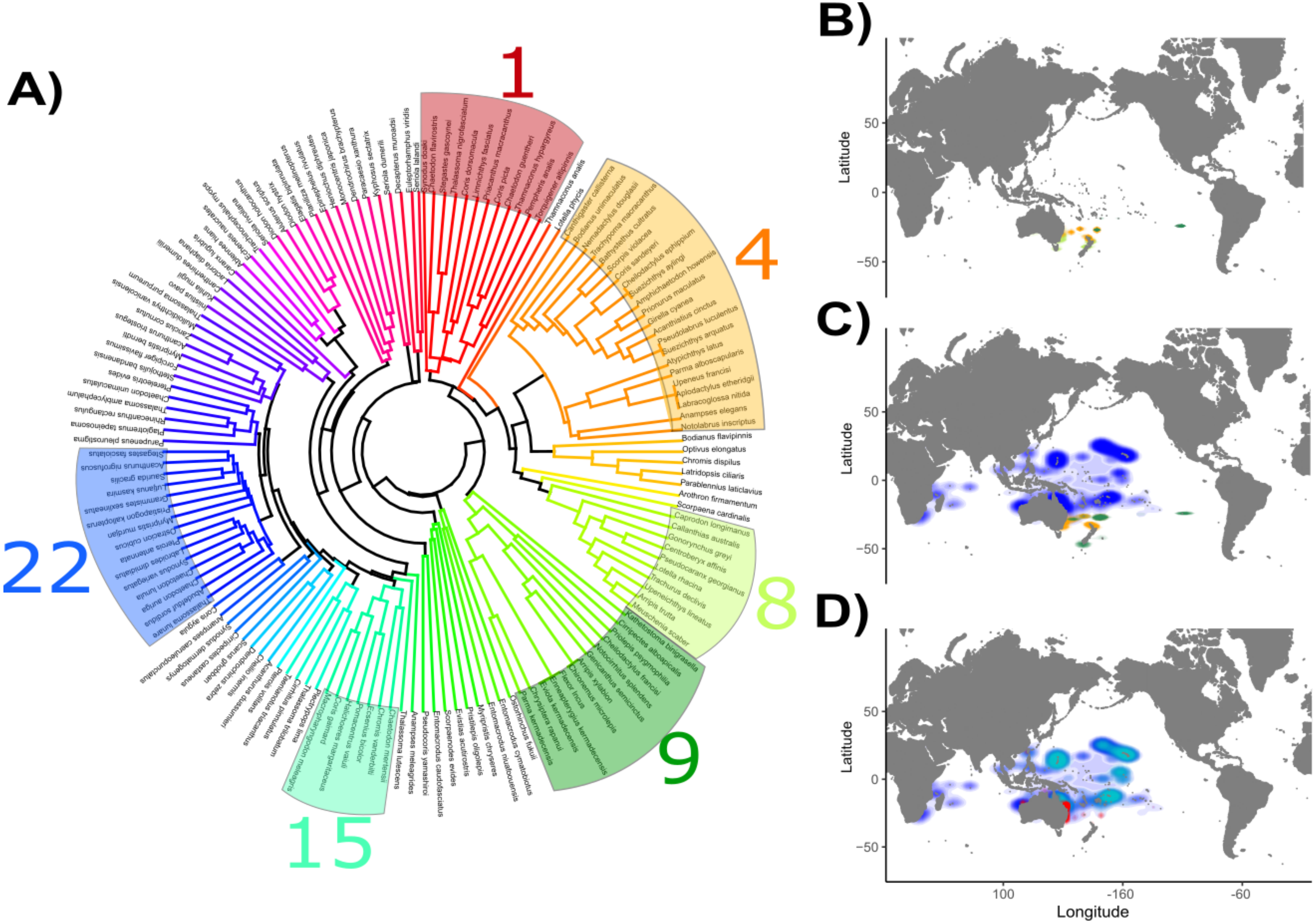

**Figure 3** (**A**) Dendrogram displaying the 32 significant biogeographic affinities for 149 species of shallow reef Teleost fishes at Rangitāhua identified by simprof analysis with geographical maps showing the kernel density estimates for the occurrences of species within the three biogeographic clusters contributing the greatest number of species in: (**B**)1980-1989 (clusters 4, 8, 9) and (**C**) 2010-2017 (clusters 4, 9, 22). (**D**) Last, the clusters with the greatest increase in their contribution to local biodiversity are shown (clusters 1, 15, 22). Changes in the kernel density for clusters is due to new species additions to in year groups (eg, cluster 9).

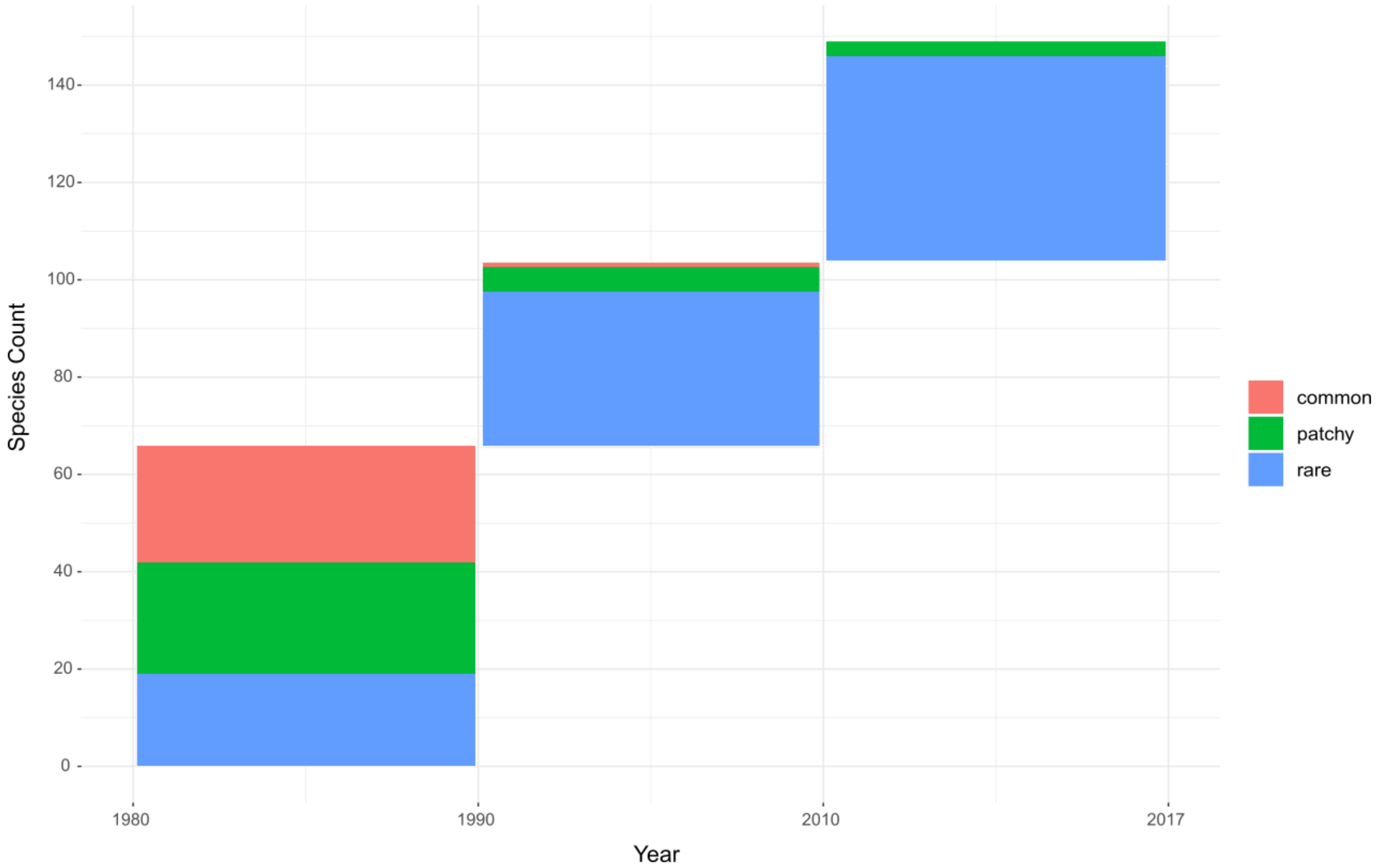

**Figure 4** Temporal changes in abundance scores (common, patchy and rare) of reef fishes at Rangitāhua over three time slots (1980-1989, 1990-1999, and 2010-2017).

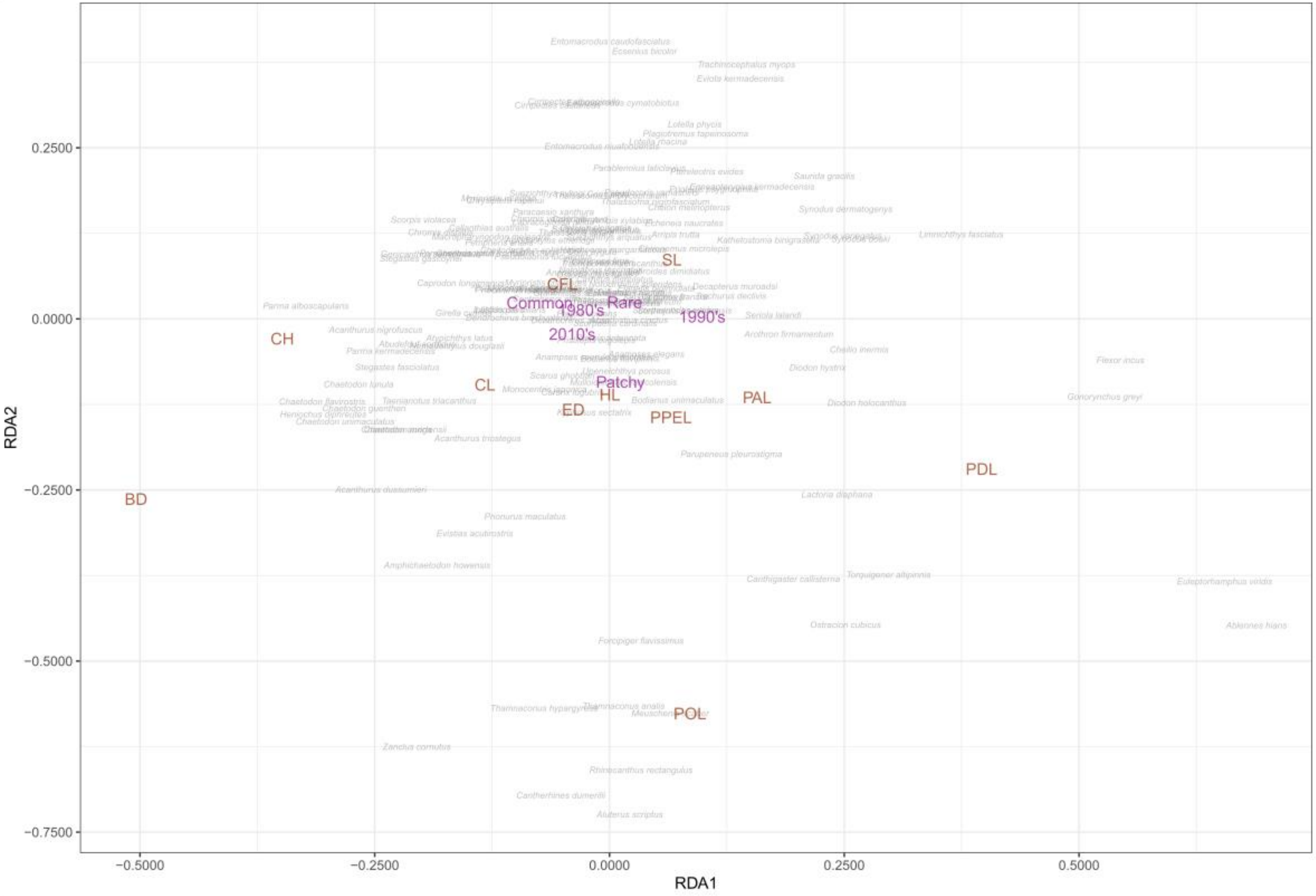

**Figure 5**
Redundancy analysis for reef fish species present at Rangitāhua with three time slots (1980-1989, 1990-1999, and 2010-2017) and three abundance categories (Common, Patchy, and Rare) plotted as explanatory variables and the centroids of the 11 standardised morphological traits: standard length (SL), head length (HL), pre-dorsal length (PDL), pre-anal length (PAL), pre-pectoral length (PPEL), eye diameter (ED), pre-orbit length (POL), body depth (BD), caudal height (CH), caudal length (CL), and caudal fork length (CFL).

# 3.5 Discussion

Using a temporally stratified list of shallow reef fish species at Rangitāhua, I identified a number of distinct biogeographic affinities for fishes contributing to the islands biodiversity. Importantly, I identified an increase in the contribution from tropical biogeographical regions over time. Despite this stronger representation, these new tropical arrivals haven't become a major component of the biodiversity yet, either due to their recent arrival or because they are at the margins of their range and environmental tolerance. Furthermore, I also detected a temporal change in morphology. However, this change in morphology was not directional; the most recent arrivals, although of a more tropical origin, have a similar morphology to the longer established, more temperate species that make up the majority of the fish fauna – in other words they appear to be temperate looking tropical fishes, possibly occupying similar niches to longer established species found around Rangitāhua.

My analysis uncovered a shift in the biogeographical affinities of shallow reef fishes for Rangitāhua. Early surveys revealed the Rangitāhua Islands have predominantly been colonised by species from higher latitude regions such as New Zealand and south eastern Australia. But more recent expeditions have found newly recorded species with biogeographic affinities to highly diverse reef areas in the Pacific Ocean and the Indo-pacific. Importantly, some of these new tropical arrivals are large bodied pelagic species (black trevally, *Caranx lugubris*) or conspicuous reef species (Bluestreak cleaner wrasse, *Labroides dimidiadus*) and therefore are unlikely to be overlooked in previous surveys. Furthermore, surveyors who participated in the expeditions during the 1980's were also involved in similar expeditions to coral reefs on Lord Howe and Norfolk Island, and therefore would be familiar with more tropical fish species should they have been present. However, it is difficult to identify whether this shift in biogeographic affinities is the impact of shifting dispersal pathways or the range extension of tropical species as a result of climate change. Support for the 'tropicalisation' of Rangitāhua would be evident in abundance changes in the resident species within its Islands, where populations of tropical species may become more prominent within the community and temperate species less abundant.

Comparing the abundance of shallow fishes revealed that species first recorded in the 1980's are also the most abundant. Most communities have more rare species than common species (Jones, Caley, & Munday, 2002), and within Rangitāhua, common shallow teleost species only covered 17% of my list while rare species constituted 62% of the species list. However, when compared to other areas such as Madagascar and French Polynesia, rare fish species constituted over 85% of the population (Harmelin-Vivien, 1989), the number of rare species in Rangitāhua is relatively low. Rare species are difficult to observe using ecological surveys (Jones *et al.*, 2002; Schiel *et al.*, 1986), but with increased effort through time, these species will eventually be found. Albeit, the rarest species recorded at Rangitāhua were often species with tropical affinities and rareness is often associated with a species being a new coloniser or a species outside of its environmental optima (Jones *et al.*, 2002; Louthan, Doak, & Angert, 2015). So, it is possible that many of these newly-recorded, rare species are new colonisers that have not had enough time to establish a steady population, or are species outside of its typical habitat, living in low population numbers but likely poised to increase in abundance should the environment change.

Although temporal changes in the biogeographical affinities were evident in newly recorded fish species, there was no associated directional temporal change in fish morphology. Shallow fishes first recorded in the 1980's shared similar morphology to fishes first recorded in the 2010's but were different from fishes first recorded in the 1990's. In particular, fishes recorded in the 1990's had shallow-elongated body shapes, while those recorded in the 1980's and 2010's had deeper bodies with larger and forked tails. The similarities in morphology between the 1980's and 2010's indicates the species recorded between these two decades may be filling similar niche spaces and using similar strategies to survive around the isolated Rangitāhua. For instance, larger forked tails are important for predator escape and prey capture (Blake, 2004; Floeter *et al.*, 2018), particularly in areas with less coral cover (Fulton, 2007). Additionally, body depth is well known to have benefits when persisting isolated environments (Jacquet *et al.*, 2017; Luiz *et al.*, 2013) and temperate islands (Feary *et al.*, 2014). Furthermore, these traits are also typical of fishes classified as common, which may indicate the importance of these traits for the isolated high latitude island setting at Rangitāhua. Thus, it is possible that tropical arrivals are exhibiting a 'temperate-like' morphology due to environmental constraints. However, over time as our climate changes, a more directional morphological change may occur with more tropical species arriving at Rangitāhua.

While my study provided an insight into the biogeographic affinities and morphological variation of the shallow fish community at Rangitāhua, I was confronted with challenges that should be mentioned. First, with collecting the data, morphological measurements for some species could not be acquired, and so I removed these species from my species list. Omission of these species could have influenced patterns; however, I feel the influence would be minimal as these species were not morphologically unique or numerous. Second, while I was able to examine the morphological change for 11 different traits, important ecomorphological traits such as gape size were not available. If specific traits were accessible, I could compare gape size change over time to identify temporal changes in functional niche space. For instance, gape size is a common trait for generalist species (Jacquet *et al.*, 2017), while a smaller mouth can correspond to tropical species with more specific niches (eg, Chaetodontidae and Acanthuridae species) (Goatley & Bellwood, 2009). Last, using abundance scores is not a completely accurate way to describe the success of a species as it does not account for behavioural characteristics. For instance, small schooling fish may more frequently appear common, while benthic ambush predatory fish will likely be rare or patchy (Connolly *et al.*, 2014). Furthermore, abundance scores do not account for larger fishes that will usually occur in low abundances due to their resource requirements to sustain their body size (White *et al.*, 2007).

My research shows there has been a temporal change in the biogeographic affinities of shallow reef fishes at Rangitāhua and even though new arrivals have more tropical biogeographic affinities, they are able to survive on the subtropical Rangitāhua archipelago because of their 'temperate' morphology. Currently, the reefs of Rangitāhua are transitional between temperate and tropical, with a mixture of macroalgal and coral substrates. Therefore, tropical arrivals are required to have traits that will ensure prey capture and predator escape for the survival of those rare individuals. However, if climate trends continue, I would expect more tropical arrivals over time with oceanographic conditions and storm events also enhancing delivery of species. Furthermore, with an influx of reef building coral species arriving, a complete change in the habitat of Rangitāhua may develop, as experienced in other parts of the world (Nakamura *et al.*, 2013; Verges *et al.*, 2014). Therefore, it is important that the fish communities of shallow reef ecosystems are monitored to provide an indication of changes dues to climate impacts, in the absence of local human interference.

# Chapter 4: General Discussion

In this thesis I describe changes in species and morphological diversity of reef fishes in relation to geography, isolation, and time. Specifically, within the Pacific Ocean, fish biodiversity shows not only a poleward decline in species richness, but more significantly, an eastward decline in species richness likely due to increasing isolation from highly diverse regions such as the Indo-Pacific 'Coral Triangle'. Furthermore, I describe an increase in the reef fish biodiversity of Rangitāhua over time, with the most recently detected species having more tropical biogeographic affinities. The increasingly tropical affinities of Rangitāhua's reef fish assemblage could be due to climate change – in which case this pattern might vary among families of fishes depending on their differing responses to any environmental change, and/or mediated by their morphology. For example, morphological changes across latitude and longitude in the Pacific, as well as morphological change over time at Rangitāhua, suggest different fish families may have different strategies for colonising remote and high latitude regions. For instance, whereas Acanthurids increased in body depth toward higher latitudes, Pomacanthids decreased in body depth but increased caudal length suggesting divergent strategies for colonising higher latitudes. Interestingly however, despite newly recorded species within Rangitāhua having tropical origins, their morphology resembled the longer established more temperate fish fauna, having larger bodies and longer caudal fins which might reduce predation risk and increase prey acquisition. Such a result suggests that rather than the fish assemblages of Rangitāhua becoming increasing 'tropical' in morphology, species colonising from tropical locations do not differ in morphology to the more temperate resident species.

Patterns of species richness within the Pacific Ocean have been well-described for numerous marine taxa (Connolly *et al.*, 2003; Edgar *et al.*, 2017; Sanciangco *et al.*, 2013). The species diversity gradient I found in my data was similar to the previously described global gradients; decreasing poleward presumably due to energy (i.e. light and temperature) (K. L. Evans *et al.*, 2005; Hawkins *et al.*, 2003), and eastwards, due to isolation (Warren *et al.*, 2015). However, even for islands at similar latitudes, the isolated region of Rangitāhua has a much lower biodiversity of reef fish when compared to Norfolk and Lord Howe Island (Francis, 2019). Nonetheless, given the young age of Rangitāhua relative to Norfolk and Lord Howe Islands, it is possible that species are still actively colonising the region. In the past few decades, biodiscovery expeditions to Rangitāhua have led to a notable increase in the number of fish known for these islands, in particular the number of fishes with more tropical affinities (Francis & Duffy, 2015). While latitudinal biodiversity gradients are well known, consequences of climate change on biodiversity across large scale gradients are beginning to be revealed as increasing numbers of species are shifting ranges towards the poles (Beare *et al.*, 2004; Davis & Shaw, 2001; Hickling *et al.*, 2006; Last *et al.*, 2011).

Increasing numbers of tropical species colonising Rangitāhua have led to a shift in the biogeographic affinity of the fish fauna consistent with 'tropicalisation'. That is, with more tropical species arriving to the subtropical area, the shallow fish assemblage appears to be transitioning from a more temperate assemblage to a tropical assemblage. But, despite occurring in low numbers, the ability of tropical species to arrive and persist in colder regions suggests climate change could be taking effect, in these high latitude islands. Other areas within the Pacific Ocean are observing similar changes with increasing numbers of species from warmer areas colonising cooler high latitudes areas (Last *et al.*, 2011; Pecl *et al.*, 2017; Verges *et al.*, 2014). Therefore, within large areas such as the Pacific Ocean, if climate change trends increase, future range shifts of tropical species towards the poles will cause a huge impact on the community structure (Assis *et al.*, 2018; Beare *et al.*, 2004; Nakamura *et al.*, 2013) and may lead to a complete change in functional trait composition within subtropical and even temperate locations (Frainer *et al.*, 2017).

I found morphological change in reef fishes of the South Pacific was more strongly associated with increasing longitude (from west to east) than increasing latitude. In accordance with other studies, the overall pattern was an increase in body size toward the eastern Pacific, most likely due to the role body size plays in increasing colonising success and persistence in remote areas (Bender *et al.*, 2017; Bender *et al.*, 2013). However, morphological changes across both latitude and longitude differed among fish families, suggesting each family may have different constraints or alternative strategies when it comes to colonising and persisting in the East Pacific. For example, Acanthurids increased in body size toward the East Pacific. Such a change in body size might reduce predation from fishes with a limited gape size (Hodge *et al.*, 2018; Nilsson & Brönmark, 2000). In contrast, other families such as Pomacanthidae and Scaridae had increased caudal length toward the East Pacific. Longer caudal fins may enable these species to out-swim predators (Blake, 2004). Additionally, morphological change in the fish assemblages of Rangitāhua over time revealed longer, taller, forked caudal fins are associated with common species (as opposed to rare species). The prevalence of longer, taller, forked caudal fins at Rangitāhua and other isolated islands within the South Pacific may be related to environmental pressures imposed on the assembly of the fish communities. For instance, with limited coral cover around Rangitāhua, there are few refuges for reef associated fishes, larger more forked caudal fins may improve accelerated swimming for predator escape and prey capture. However, with increasing sea surface temperatures, high latitude islands are becoming more habitable for reef building coral and should these species extend ranges or become more abundant, we may find that tropical fish species may become more common at

Rangitāhua and other high latitude islands influencing morphological diversity within the fish assemblages.

Here, I combined new empirical data and pre-existing data available from open source databases. Although extensive quality control was undertaken on all retrieved data, the data has some limitations. First, the morphological measurements collected from fishbase were only available in units of pixel length, as opposed to absolute measurements. To enable comparison among species, and assemblages, all species measurements were standardised (by either head length or total length). This transformation meant I could examine relative proportional changes in morphology, and not absolute changes. For example, in a case where there was an increase in head length across the gradient, but no change in eye diameter, in my data this would appear as a decrease in eye diameter. Second, although I was able to examine changes in many morphological traits, several trait measurements of known ecomorphological importance (Villéger *et al.*, 2017) were not available from the databases I queried. In the absence of a measurement specifically related to gape size for example, I presumed that a relative increase in head length and/or pre-orbit length was indicative of changes in relative gape size. However, accurately identifying changes in gape size directly would provide better understanding of likely dietary changes across latitude, longitude and over time. Third, the abundance scores used in Chapter 3 may not accurately reflect the success of species at Rangitāhua, as some species are naturally more rare than others, depending on resource use, behavioural characteristics, life-history strategies, and/or biomass. For instance, small schooling fish will appear common, while larger territorial predatory fishes will usually occur in low abundance due to their required resource intake (Connolly *et al.*, 2014; White *et al.*, 2007). Regardless of these caveats, my analysis presents previously undescribed longitudinal patterns of morphological change among families, a dramatic shift in biogeographic affinities for the fish assemblages of Rangitāhua and an unexpected result where the morphology of recently colonising tropical species closely resembled that of resident temperate fishes.

As our climate changes and enhances, modifies and obscures ocean barriers, future research should monitor and identify biodiversity shifts and changes in morphological diversity across large-scale geographic gradients such as longitude and latitude. Furthermore, it is important to acknowledge that marine protected areas will not be immune to such change. Specifically, monitoring of Rangitāhua's biodiversity, a location with zero or negligible local anthropogenic impacts, could provide insight into climate induced range shifts that may be expected in mainland New Zealand and across the broader Pacific Ocean. Moreover, extending temporal monitoring of fish assemblages to other isolated islands within the Pacific Ocean will allow us to compare and contrast the recent, or real-time, impacts of climate change across largescale gradients.

Furthermore, using similar methods as to what I have done here, but focusing on identifying intraspecific morphological variation among populations would provide insight into the environmental and selective pressures driving local adaptation and morphological change within populations. Whether these population changes are similar in direction to the changes I detected at the assemblage level would reveal whether contemporary pressures are the same as those that have shaped the shallow reef fish assemblages over longitude, latitude and time. Additionally, future studies on target species will allow us to better manage climate induced impacts on fisheries. In particular, identifying changes in functional traits associated with feeding, behaviour, and fecundity would allow us to make decisions for better managing fisheries. Within the Pacific Ocean numerous islands depend on fisheries for the survival of their community, and so managing these resources is of upmost concern for local populations.

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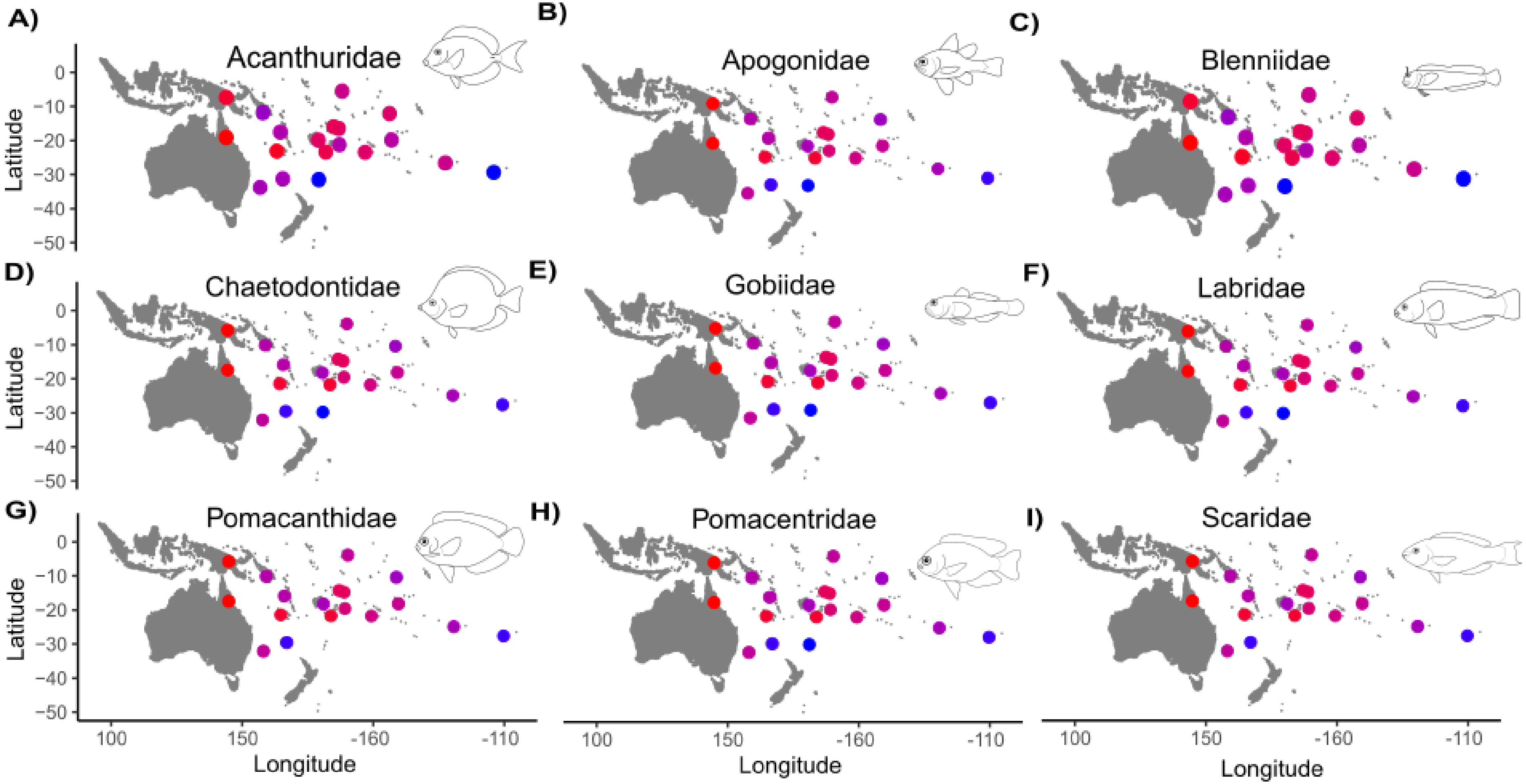
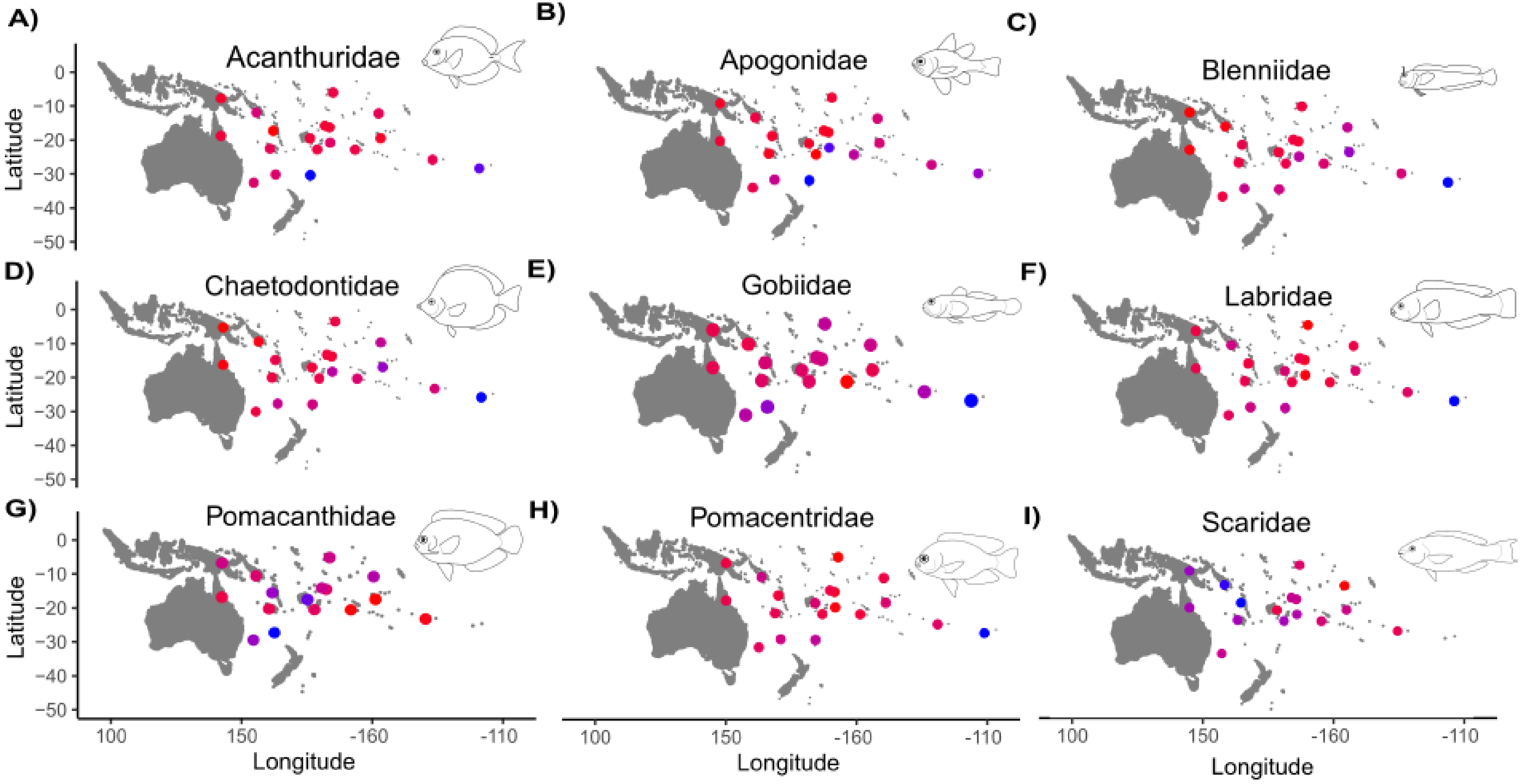
# Appendices

| | Acanthurid | Prop. | Apogonid | Prop. | Blenni | Prop. | Chaetodon | Prop. | Gobi | Prop. | Labrid | Prop. | Pomacanthid | Prop. | Pomacentrid | Prop. | Scarid | Prop. | **TOTAL** | **Prop.** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| American Samoa | 0 | 0 | 4 | 0.19 | 3 | 0.09 | 1 | 0.045 | 9 | 0.243 | 0 | 0 | 0 | 0 | 1 | 0.047 | 1 | 0.045 | **19** | **0.078** |
| Australia | 4 | 0.085 | 29 | 0.239 | 17 | 0.215 | 1 | 0.02 | 122 | 0.414 | 22 | 0.138 | 4 | 0.153 | 7 | 0.052 | 2 | 0.062 | **208** | **0.221** |
| Caroline Island | 1 | 0.033 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0.272 | 0 | 0 | 0 | 0 | 1 | 0.05 | 0 | 0 | **5** | **0.043** |
| Cook Islands | 1 | 0.033 | 1 | 0.142 | 2 | 0.125 | 2 | 0.125 | 5 | 0.312 | 3 | 0.057 | 1 | 0.09 | 2 | 0.058 | 2 | 0.111 | **19** | **0.095** |
| Easter Island | 0 | 0 | 1 | 0.142 | 0 | 0 | 2 | 0.222 | 4 | 0.666 | 2 | 0.166 | 0 | 0 | 0 | 0 | 0 | 0 | **9** | **0.195** |
| Fiji | 1 | 0.032 | 17 | 0.236 | 9 | 0.183 | 1 | 0.03 | 36 | 0.327 | 3 | 0.061 | 2 | 0.181 | 3 | 0.048 | 1 | 0.1 | **73** | **0.17** |
| Kermadec Islands | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 3 | 0.157 | 0 | 0 | 2 | 0.333 | 0 | 0 | **7** | **0.159** |
| Kiribati | 0 | 0 | 5 | 0.25 | 2 | 0.064 | 1 | 0.05 | 9 | 0.281 | 4 | 0.097 | 0 | 0 | 2 | 0.052 | 1 | 0.071 | **24** | **0.104** |
| Lord Howe Island | 1 | 0.062 | 0 | 0 | 1 | 0.062 | 0 | 0 | 8 | 0.32 | 3 | 0.053 | 2 | 0.222 | 1 | 0.031 | 1 | 0.071 | **17** | **0.082** |
| New Caledonia | 1 | 0.024 | 18 | 0.214 | 7 | 0.111 | 1 | 0.029 | 45 | 0.269 | 12 | 0.095 | 1 | 0.047 | 3 | 0.024 | 2 | 0.071 | **90** | **0.131** |
| Niue | 1 | 0.055 | 0 | 0 | 2 | 0.285 | 1 | 0.1 | 1 | 0.5 | 2 | 0.09 | 0 | 0 | 0 | 0 | 1 | 0.052 | **8** | **0.089** |
| Norfolk Island | 1 | 0.062 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0.428 | 3 | 0.103 | 0 | 0 | 1 | 0.052 | 0 | 0 | **8** | **0.076** |
| Papua New Guinea | 3 | 0.073 | 26 | 0.23 | 16 | 0.197 | 1 | 0.02 | 99 | 0.405 | 11 | 0.081 | 4 | 0.148 | 12 | 0.096 | 1 | 0.032 | **173** | **0.204** |
| Pitcairn Islands | 1 | 0.041 | 1 | 0.1 | 0 | 0 | 3 | 0.166 | 3 | 0.23 | 2 | 0.052 | 0 | 0 | 1 | 0.05 | 1 | 0.1 | **12** | **0.075** |
| Samoa | 1 | 0.03 | 4 | 0.117 | 7 | 0.142 | 2 | 0.068 | 12 | 0.169 | 2 | 0.03 | 0 | 0 | 1 | 0.019 | 1 | 0.045 | **30** | **0.081** |
| Solomon Islands | 0 | 0 | 11 | 0.183 | 10 | 0.222 | 0 | 0 | 34 | 0.311 | 6 | 0.122 | 3 | 0.187 | 6 | 0.064 | 1 | 0.083 | **71** | **0.172** |
| Tahiti | 1 | 0.05 | 2 | 0.2 | 1 | 0.166 | 0 | 0 | 8 | 0.47 | 2 | 0.083 | 1 | 0.111 | 0 | 0 | 1 | 0.066 | **16** | **0.13** |
| Tonga | 1 | 0.028 | 9 | 0.166 | 10 | 0.188 | 1 | 0.028 | 27 | 0.247 | 6 | 0.067 | 2 | 0.111 | 3 | 0.039 | 2 | 0.071 | **61** | **0.122** |
| Vanuatu | 1 | 0.055 | 4 | 0.166 | 5 | 0.2 | 0 | 0 | 15 | 0.333 | 3 | 0.075 | 2 | 0.125 | 2 | 0.025 | 1 | 0.083 | **33** | **0.116** |
| **TOTAL** | **19** | **0.04** | **132** | **0.197** | **92** | **0.154** | **17** | **0.039** | **445** | **0.337** | **89** | **0.083** | **22** | **0.103** | **48** | **0.05** | **19** | **0.063** | **883** | **0.146** |

**Appendix 1** Number and proportion of species removed from the overall data for my nine families (Acanthuridae, Apogonidae, Blenniidae, Chaetodontidae, Gobiidae, Labridae, Pomacanthidae, Pomacentridae, and Scaridae) across the nineteen locations (American Samoa, Australia, Caroline Island, Cook Islands, Easter Island, Fiji, Karmadec Islands, Kiribati, Lord Howe Island, New Caledonia, Niue, Norfolk Island, Papua New Guinea, Pitcairn Islands, Samoa. Solomon Islands, Tahiti, Tonga, Vanuatu).



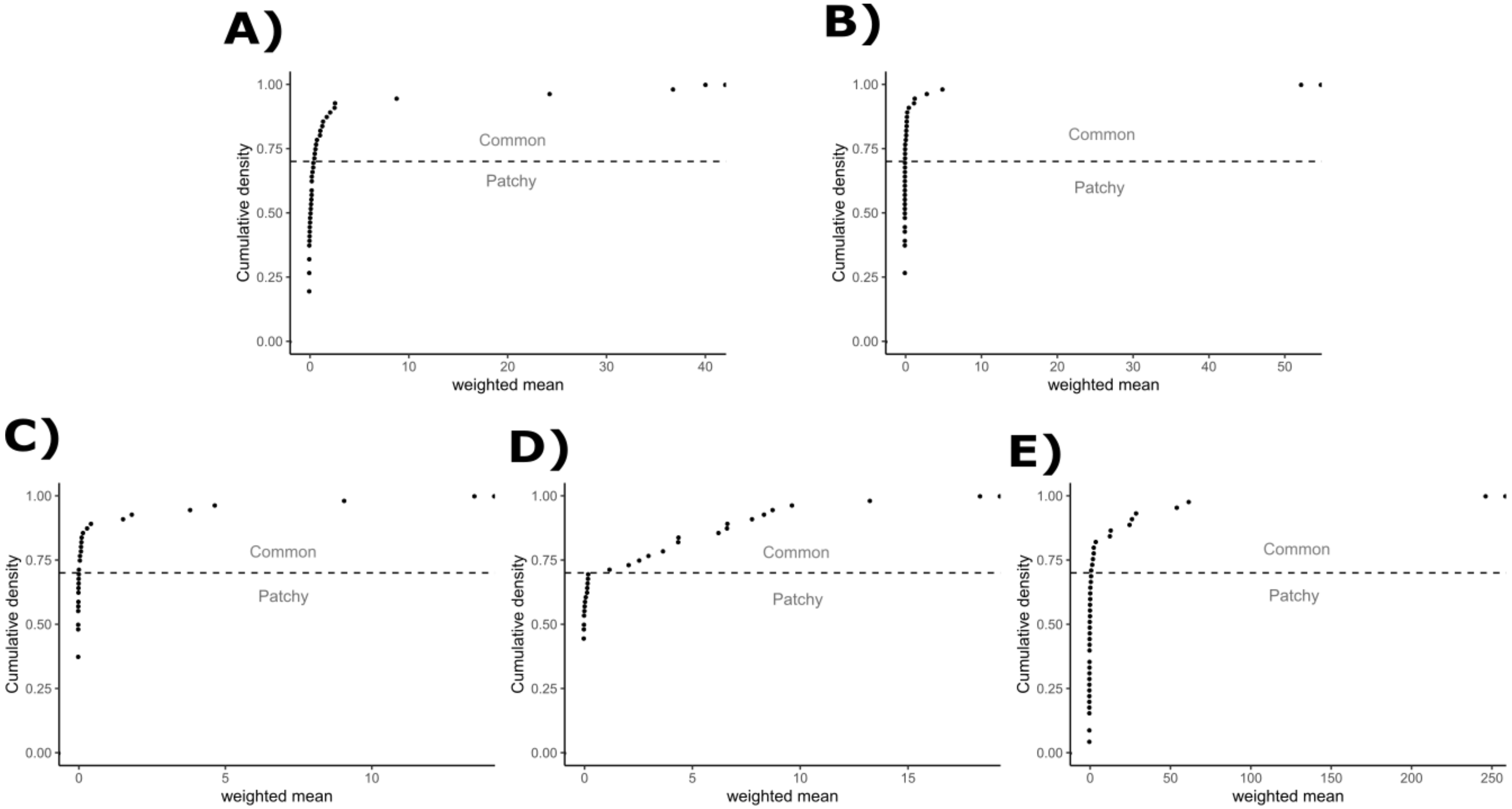
**Appendix 2** Species richness for nine reef fish families within the South Pacific: **A**) Acanthuridae, **B**) Apogonidae, **C**) Blenniidae, **D**) Chaetodontidae, **E**) Gobiidae, **F**) Labridae, **G**) Pomacanthidae, **H**) Pomacentridae, **I**) Scaridae. Warm colours indicate high species richness.



**Appendix 3** Morphological diversity (beta dispersions for the Euclidean distances among 13 morphological traits see Methods for more details) for nine reef fish families within the South Pacific: **A**) Acanthuridae, **B**) Apogonidae, **C**) Blenniidae, **D**) Chaetodontidae, **E**) Gobiidae, **F**) Labridae, **G**) Pomacanthidae, **H**) Pomacentridae, **I**) Scaridae. Warm colours indicate high morphological diversity.

|  | $P_{(\text{perm})}$ |  | $P_{(\text{perm})}$ |  |
|---|---|---|---|---|
|  | RDA1 | RDA2 | Latitude | Longitude |
| Acanthuridae | 0.0862 | 0.2972 | 0.0764 | 0.146 |
| Apogonidae | 0.431 | 0.5749 | 0.4914 | 0.1769 |
| Blenniidae | 0.0779 | 0.9968 | 0.9088 | 0.0702 |
| Chaetodontidae | 0.2365 | 0.7957 | 0.3437 | 0.3149 |
| Gobiidae | 0.6767 | 0.99 | 0.9332 | 0.6142 |
| Labridae | 0.0147 | 0.0113 | 0.0052 | 0.0063 |
| Pomacanthidae | 0.0053 | 0.9721 | 0.4449 | 0.0087 |
| Pomacentridae | 0.1843 | 0.8512 | 0.6996 | 0.1401 |
| Scaridae | 0.7678 | 0.9846 | 0.9763 | 0.4493 |

**Appendix 4** Permutational P-values for the constrained axes (RDA1 and RDA2) and the constraining variables (Latitude and Longitude) for the nine reef fish families displayed in figure 6 (for more details see Results 2.4.2).



**Appendix 5** Culuative density pltos of weighted mean abundance scores for five qunatitiative fish surveys conducted at Rangitāhua: Trnski T. *unpublished* (**A**), Liggins et al. 2020 (**B**), Eddy 2011 (**C**), Duffy C. *unpublished* (**D**), and Reef Life Survey (Edgar & Stuart-Smith, 2019; 2014) (E). The horizontal dotted line indicates the 70th percentile cut-off we used to distinguish common (above the cut-off) and patchy (below the cut-off) species.